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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XLI, No. 6, pp. 215–231; 17 figs.; 1 table August 18, 1977

SYSTEMATICS AND BIOLOGY OF THE DEEP-SEA FISH FAMILY GIBBERICHTHYIDAE, A SENIOR SYNONYM OF THE FAMILY KASIDOROIDAE[1]

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ABSTRACT: The fish family Kasidoroidae Robins and de Sylva (1965) is shown to be based on Atlantic specimens of the unusual prejuvenile stage of the xenoberyciform genus *Gibberichthys* Parr (1933). *Kasidoron edom* Robins and de Sylva (1965) is treated as the prejuvenile stage of *Gibberichthys pumilus* Parr (1933). *Kasidoron latifrons* Thorp (1969), described from a prejuvenile specimen from the western Indian Ocean, is confirmed to be a separate species, *G. latifrons*; it is now known from the Indian Ocean and the western and southwestern parts of the Pacific Ocean. Ontogenetic changes from the larval stage to the adult are discussed and illustrated for *G. pumilus*, particularly the development and loss of the pelvic appendage—a modified third pelvic fin ray—and the development of crests on the head. The prejuvenile stage is found in epipelagic waters, and adults apparently occur in the lower mesopelagic and perhaps upper bathypelagic levels; adults probably do not undergo daily vertical migration. Additional notes on biology are included.

INTRODUCTION

A new family of fishes, the Kasidoroidae, was established by Robins and de Sylva (1965) for a small western Atlantic species characterized by a peculiar pelvic appendage, a modified third pelvic fin ray. They included the family in the order Mirapinniformes. Robins (1966) provided additional comments on the family and order. Myers and Freihofer (1966) compared the family Kasidoroidae (incorrectly spelled by them as Kasidoridae) with their family Megalomycteridae. Greenwood et al. (1966) listed the family Kasidoridae (*sic*) in the suborder Mirapinnatoidei, order Cetomimiformes. However, Rosen and Patterson (1969: 456) suggested that, "from illustrations of this fish [*Kasidoron edom*] and a brief examination of the holotype we are convinced that it is very closely related to, and may be only the larva of, the beryciform *Gibberichthys pumilus*, with which it agrees in al-

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[1] Contribution from the University of Miami, Rosenstiel School of Marine and Atmospheric Science. Biological Results of the University of Miami Deep-Sea Expeditions No. 122. This research was supported in part by National Science Foundation research grants GB-893, GB-4472, GB-8047 to the senior author, by research grant OCE 76-02251 to Dr. Bruce Robison, and by Biological Ship Time grants GB-1204 and GA-4569.

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most every character. . . . *Kasidoron* is therefore a beryciform. . . .'' Rosen and Patterson did not elaborate further. A second species of *Kasidoron, K. latifrons*, was described by Thorp (1969) from off Zanzibar in the western Indian Ocean.

During the period 1969–1972, we were able to examine specimens referable to *Kasidoron edom* collected since the description of that species and many adult specimens identifiable as *Gibberichthys pumilus*. Our study of these specimens confirmed that *Kasidoron edom* indeed represented the prejuvenile stage of *Gibberichthys pumilus*, and we were thus able to trace ontogenetic changes and to provide information on biology and distribution. Our paper was ready to publish in 1972 and was cited as in press by Ebeling and Weed (1973: 412, footnote) in their treatment of the family Gibberichthyidae in the series titled "Fishes of the western North Atlantic." One dilemma caused us to withhold the paper at that time—this involved specimens from areas other than the Atlantic. At that time (1972) we had an adult specimen from the western Indian Ocean and a small postlarval specimen from the Molucca Sea. The adult was not in good condition and the description of *latifrons* was based on a prejuvenile which seemed to be somewhat different from the Atlantic prejuveniles available to us. Was *latifrons* a separate species?

In 1973 Dr. John Paxton made available to us an adult specimen in excellent condition which was collected from the south-central Pacific, and, as noticed by Dr. Paxton, his specimen seemed to differ noticeably from Atlantic adults in having smaller scales, among other features. In 1975 Dr. Bruce Robison made available to us an adult collected in the Halmahera Sea during the R/V Alpha Helix S.E.A.L. Expedition; he subsequently provided a second specimen from the same source. Recently Paxton informed us of an adult specimen in good condition collected by the R/V Galathea off Madagascar which he located in the Zoological Museum in Copenhagen. At last it was possible to compare an adult in good condition from the western Indian Ocean (type locality of *latifrons* was off Zanzibar) with adults from the Pacific and with *G. pumilus* in the Atlantic and to evaluate the status of *latifrons*.

ACKNOWLEDGMENTS

We thank Dr. E. Bertelsen and officials of the Danish Dana Oceanographic Collections for making available four postlarval specimens and facilities for use by the senior author during a visit to Copenhagen in 1969. The National Marine Fisheries Service, Exploratory Fishing and Gear Research Base, Pascagoula, Mississippi, provided most of the Atlantic adult specimens, particularly through the efforts of Mr. Edward Klima and Mr. Bennie Rohr. Dr. John Paxton, Australian Museum, Sydney, made available an adult specimen collected by the ORSTOM Center at Noumea, New Caledonia; Drs. Paxton and P. Fourmanoir (ORSTOM) kindly allowed us to utilize information in their unpublished manuscript on this specimen. Dr. Paxton also brought to our attention the existence of an adult specimen in the Zoological Museum of the University of Copenhagen collected by the Galathea off Madagascar; this specimen was loaned to us by Dr. Jørgen Nielsen. Dr. Bruce Robison, University of California, Santa Barbara, made available two adults collected by the R/V Alpha Helix in the Halmahera Sea. Dr. Leslie Knapp, Smithsonian Oceanographic Sorting Center, generously made available an adult from the western Indian Ocean. Mrs. Myvanwy Dick, Museum of Comparative Zoology, Harvard University, loaned specimens. The staff of the U.S. National Museum of Natural History aided the junior author while he was examining specimens in their care. Most postlarval specimens from the Atlantic resulted from the cooperation of the officers and crew of the University of Miami's R/V Pillsbury. Dr. William M. Stephens greatly assisted in the early stages of preparation of this manuscript and with cinemaphotography of a living specimen. Mrs. Ann Jensen and Mr. Richard Schekter were especially helpful in assisting the senior author during Pillsbury cruise P-6907. Mr. Schekter and Mr. Kenneth Kimball kindly examined stomach contents of Atlantic specimens. Mrs. Fay Mucha prepared histological sections of an adult. Discussions about this study with Dr. C. Richard Robins were of much assistance. We are especially grateful to Ms. Joy Godfrey for preparing the drawings of the fish. Drs. C. Richard Robins, Warren Freihofer, John Paxton, and Robert K. Johnson, and Mrs. Lillian Dempster offered suggestions on all or parts of early drafts of the manuscript. Mrs. Katherine Smith, Mrs. Terry Arambula Greenfield, Mr. James Gordon, Mr. Maurice Giles, Mr. Donald Heuer, Ms. Terry Loy, Mr. William Ruark, and Miss Pearl Sonoda aided in various ways. Mrs.

ca Abbott gave us valuable editorial assis- .

METHODS

: prejuvenile specimens are here termed the doron'' stage, although subsequent work- ay wish to disregard this term. The kasido- tage is characterized by the presence of a ıe pelvic appendage, and we confine the to specimens possessing the appendage. terminology "prejuvenile" comes from ›s (1958) as modified by Mansueti and Hardy).

e last two elements in the dorsal and anal fin ɔunted as one ray. The first elements in the ıl and anal fin become spinous when the fish :ween 20 and 30 mm standard length (SL). fin-ray counts of adults are taken as the ›er of spinous points or spines plus soft rays :ext).

:asurements are those commonly used to ibe teleost fishes with a few modifications. ıurements originating from the anterior end : fish are taken from the most anterior point : left premaxillary. Head length is measured e posteriormost tip of the upper opercular . Orbit diameter is the interior diameter of ›ony orbit measured in a horizontal line. ıurements of prejuvenile specimens were : with an ocular micrometer. The third pelvic ; measured to the tip of the ray without the c tree, and the stalk of the pelvic tree is ured from the tip of the pelvic ray to the end e main stalk. Many adults were variously ıged during capture, and some mea- nents are, therefore, inaccurate. Mea- nents of adults were usually taken to the :st 0.5 mm. Original data used to prepare 'es 8–13 are on file at the California lemy of Sciences.

ıbreviations of depositories of specimens are llows: AMNH—American Museum of Nat- History, New York; AMS—Australian :um, Sydney; ANSP—Academy of Natural nces of Philadelphia; BMNH—British :um (Natural History), London; BOC— ham Oceanographic Collection, Yale Uni- ty; CAS—California Academy of Sciences, Francisco; MCZ—Museum of Comparative ɔgy, Harvard University; SIO—Scripps In- ion of Oceanography, La Jolla; UMML— ersity of Miami, Rosenstiel School of ne and Atmospheric Science, Miami; USNM—United States National Museum of Natural History, Washington, D.C.; ZMUC—Zoological Museum, University of Copenhagen.

MATERIAL EXAMINED

(Number of specimens and their standard length [mm] in parentheses.)

Gibberichthys pumilus

Kasidoron stage (depths of capture are as given by the collecting agency and are approximate estimates based on wire out and wire angle; these specimens were collected with 1-meter and 2-meter plankton nets): ANSP 102061 (1; 21.2, holotype of *K. edom*), 28°27′ to 28°25′N, 73°42′W, 15 m over bottom of 4462 m, Pillsbury sta. 165, 2235–2335 hrs, 7 Aug. 1964. ANSP 102062 (1; 15.7, paratype of *K. edom*), taken with the holotype. UMML 16213 (1; 7.8, paratype of *K. edom*), 32°46′N, 64°33′W, 8 m over 2743 m, Pillsbury sta. 144, 2025–2115 hrs, 3 Aug. 1964. UMML 16214 (1; 12.1, paratype of *K. edom*), 28°30′ to 28°27′N, 73°39′ to 73°42′W, 1–2 m over 4462 m, Pillsbury sta. 164, 2115–2215 hrs, 7 Aug. 1964. UMML 28806 (1; 15.3), 30°00′N, 68°00′W, 16 m over 5014 m, Pillsbury sta. 1053, 2109–2143 hrs, 24 Aug. 1969. ZMUC P41630 (1; 7.5), 21°50′N, 50°12′W, 100 m wire out, Dana sta. 3543 III, 2145 hrs, 12 Aug. 1928. ZMUC P41631 (1; 9.0), 24°48′N, 53°47′W, 17 m wire out, St. Jan sta. 543, 1930 hrs, 6 Aug. 1912. ZMUC P41632 (1; 11.1), 24°10′N, 67°00′W, 77 m wire out, Ag Peterson sta. 803, 1900 hrs, 21 Sept. 1914.

Adults: CAS 14564 (2; 69 and 87, cleared and stained), 7°41′N, 53°48′W, 677 m, Oregon II sta. 10606, 21-m shrimp trawl, 10 May 1969. CAS 14565 (3; 49, 53, and 71.5) and BMNH (1; 57.5), 29°16′N, 86°55′W, 640 m, Oregon II sta. 10913, 58-m shrimp trawl, 12 Feb. 1970. FMNH 82924 (1; 80.5), 7°49′N, 54°22′W, 732 m, Oregon II sta. 10604, 21-m shrimp trawl, 10 May 1969. CAS 14566 (1; 91.5), 17°42′N, 63°58′W, 741 m, Oregon II sta. 10832, 21-m shrimp trawl, 3 Dec. 1969; CAS 37920 (1; 85), 7°41′N, 53°57′W, 735 m, Oregon II sta. 10621, 30-m shrimp trawl, 16 May 1969. CAS 14567 (2; 63 and 78) and CAS 14568 (1; 82.5, nerve preparation), 7°35′N, 53°29′W, 658 m, Oregon II sta. 10608, 39-m shrimp trawl, 11 May 1969. CAS 14569 (1; 85.5), 29°09′N, 87°58′W, 841 m, Oregon II sta. 10650, 68-m shrimp trawl, 25 June 1969. CAS 14570 (1; 83.5) and UMML 7041 (4; 57, 72.5 82.0, and 83.5), 29°10′N, 87°55′W, bottom depth 933–732 m (fishing depth uncertain), Oregon sta. 2399, 12-m mid-water trawl, 4 Feb. 1959.

The following additional adults were used in the map of distribution but were not examined in detail: MCZ 44211 (3 specimens), 7°46′N, 54°00′W, 732 m, Oregon sta. 4299, 20-m shrimp trawl, 23 Mar. 1963. USNM 187664 (1), 29°54′N, 80°11′W, 320–329 m, Silver Bay sta. 3661, 24-m flat trawl, 16 Jan. 1962. UMML uncat. (1; frozen), 20°40′ to 20°42′N, 73°48′ to 73°40′W, est. depth 800–1100 m over 1463–2304 m, Pillsbury sta. 1174, midwater trawl, 0441–0945 hrs, 29 June 1970. USNM 187665 (1), 29°11′N, 87°47′W, 832 m, Oregon sta. 3218, 18/24-m semi-balloon trawl, 9 Feb. 1961. Plus literature reference to one from Oregon sta. 1425, 29°04′N, 88°05′W, 914 m, 24 Sept. 1955. Plus the following USNM uncat. lots: Oregon sta. 3654 (1), 29°08.5′N, 88°00.5′W, 732–750 m, 12-m flat trawl, 25 July 1962. Oregon sta. 3660 (1), 29°10′N, 87°57′W, 658–732 m, 12-m flat trawl, 27 July 1962. Oregon sta. 3669 (1), 28°51.5′N, 88°39′W, 622 m, 12-m flat trawl, 29 July 1962. Oregon sta. 3670 (4), 29°00.5′N, 88°22′W, 732 m, 12-m flat trawl, 30 July 1962. Oregon sta. 4902 (2), 09°02.4′N, 76°31.5′W, 732 m, 20-m shrimp trawl, 28 May 1964. Miss Virginia, no sta. (1), 29°10′N, 79°50′W, 180–200 m, Mar.–Apr.

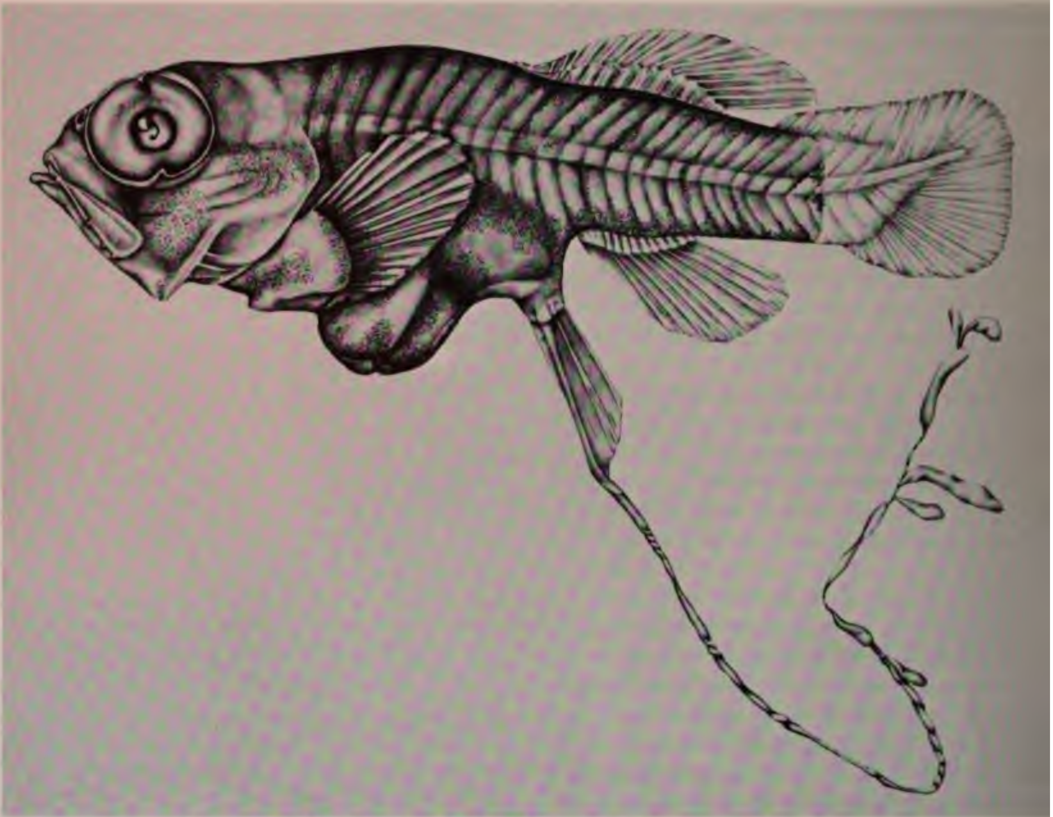

FIGURE 1. *Gibberichthys pumilus*, kasidoron stage, 7.5 mm SL, ZMUC P41630.

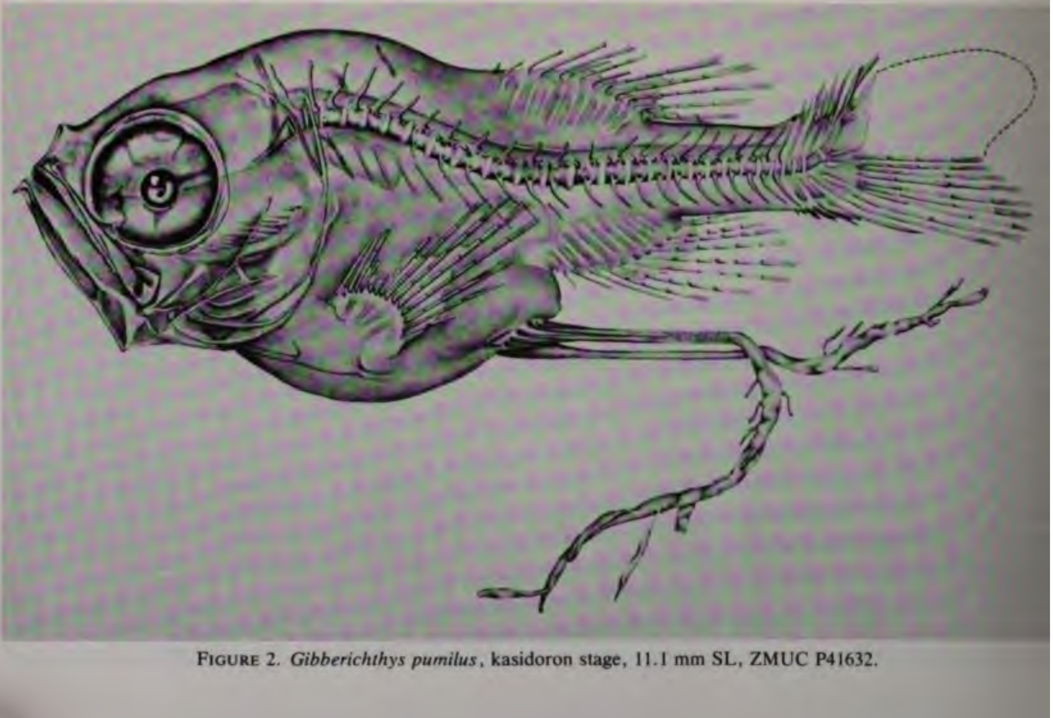

FIGURE 2. *Gibberichthys pumilus*, kasidoron stage, 11.1 mm SL, ZMUC P41632.

s the specimens reported by Parr (1933): BOC 2838 (1; otype of *G. pumilus*) 21°44′N, 72°43′25″W, 2134 m wire vnee sta. 48, about 2127 hrs, 6 Apr. 1927. BOC uncat. 5°39′N, 77°18′W, 1050 or 1100 m to surface, triangular r trawl, Atlantis sta. 1478, 20–21 Feb. 1933.

hthys latifrons

oron stage: ZMUC P41633 (1, 7.8), 2°17′N, 126°48.5′E, vire out, Dana sta. 3744 V, 2110 hrs, 7 July 1929. (Plus description of *K. latifrons*, type locality off Zanzibar.) s: USNM 205551 (1; 112), 16°44′S, 43°44′E, 58 m, rawl, Anton Bruun cruise 8, sta. 407J, 15 Oct. 1964. 41634 (1; 124), off Madagascar, 11°43′S, 49°09′E, 1300 thea Expedition 1950–52, sta. 220, 1 Mar. 1951. AMS 001 (1; 103), 11°17′S, 142°47′W, 0–1040 m, 3-m IKMT, M) Coriolis sta. Caride III-17, 7–8 Feb. 1969. CAS ; 80), Halmahera Sea, 0°10.5′S, 128°33.3′E, 750–1000 ing and closing 2.4-m Robison midwater trawl, Alpha S.E.A.L. Expedition, sta. 142, 1200–1400 hrs, 20 May AS 37919 (1; 89.6), Halmahera Sea, 0°08.9′S, ′E, 0–960 m, 2.4-m Robison midwater trawl, Alpha S.E.A.L. Expedition, sta. 137, 0955–1300 hrs, 19 May

OMPARISON OF *KASIDORON EDOM* WITH *GIBBERICHTHYS PUMILUS*

ugh a complete size series of specimens is ailable, it is possible to show that *Kasido-* *dom* is the prejuvenile stage of *Gib-* *thys pumilus*. Evidence comes especially netamorphosis of the pelvic appendage, nation of ontogenetic changes in the devel- nt of crests on the head, similarity of meris- tures, and other characters. These are dis- d below.

appendage.—The most striking feature of sidoron stage is the presence of a peculiar appendage (pelvic arborescence of Robins Sylva 1965). This structure is described in by Robins and de Sylva (1965) and Robins . The pelvic appendage is a highly modified elvic ray which, according to Robins and va (1965: 192), is "... fitted at its tip with a ound stalk to which attach large, hollow, e sacs." The pelvic appendage they illus- was partially reconstructed and seems to een an even larger arborescence (see also 1969, Fig. 1, for *G. latifrons*). Additional al available to us shows the development structure (Figs. 1–3). The pelvic tree is artially developed in the 7.5-mm specimen) and an 11.1-mm specimen (Fig. 2), and it roliferates rapidly in size and complexity as in a 15.3-mm specimen (Fig. 3). (Further ishment is found in the 21.0-mm holotype of *Kasidoron latifrons* [Thorp 1969: Fig. 1].) The 31.5-mm holotype of *Gibberichthys pumilus* lacks the pelvic appendage, as do all of our larger specimens. However, we do find evidence in adults which suggests the fate of the pelvic appendage. In adults there is a discontinuity area part way up the third pelvic fin ray (Fig. 4) which is easily visible in cleared-and-stained specimens. We believe the expanded area represents the site of attachment of the pelvic appendage. It seems most likely that when the pelvic tree is lost the third pelvic ray continues to grow and segment normally, producing the result shown in Fig. 4. This discontinuity occurs only on the third pelvic ray as evidenced by examination of three cleared-and-stained specimens. The third pelvic ray in most juveniles and adults shows some evidence of deformity; it is the thickest, and is frequently slightly bent or distorted. The pelvic appendage is lost when the fish is between about 21 and 31 mm standard length, the limits of our material which have or do not have the appendage.

Body shape and coloration.—The 15.3-mm prejuvenile specimen (Fig. 3), the 31.5-mm holotype of *Gibberichthys pumilus* (Fig. 5), and large adults (Figs. 6 and 7) show the changes in body shape with growth. Measurements (Figs. 8–13) reveal that there is a constant growth rate of most body parts when compared with standard length, but different slopes of the growth curves cause different apparent effects. For example, the orbit increases in diameter very slowly as the fish grows, so that the orbit is nearly one-half the head length in prejuvenile specimens but one-seventh or one-eighth of the head length in adults. Measurements of some body parts when plotted against standard length show slight changes in growth rates at about a size where the pelvic appendage is lost, and presumably when the juvenile specimens move to a deeper habitat. For example, the snout length (Fig. 11) grows slowly in prejuvenile specimens, subsequently increases rapidly, and then shows a slower constant growth rate in adults. Head length (Fig. 13) seems to show a similar change in growth rate. The length of the third pelvic fin ray (Fig. 12) increases very slowly, thereby becoming very small proportionally in larger specimens, but some variability in our measurements results from the third ray being broken in large specimens; the development of the pelvic appendage (Fig. 12) is ex-

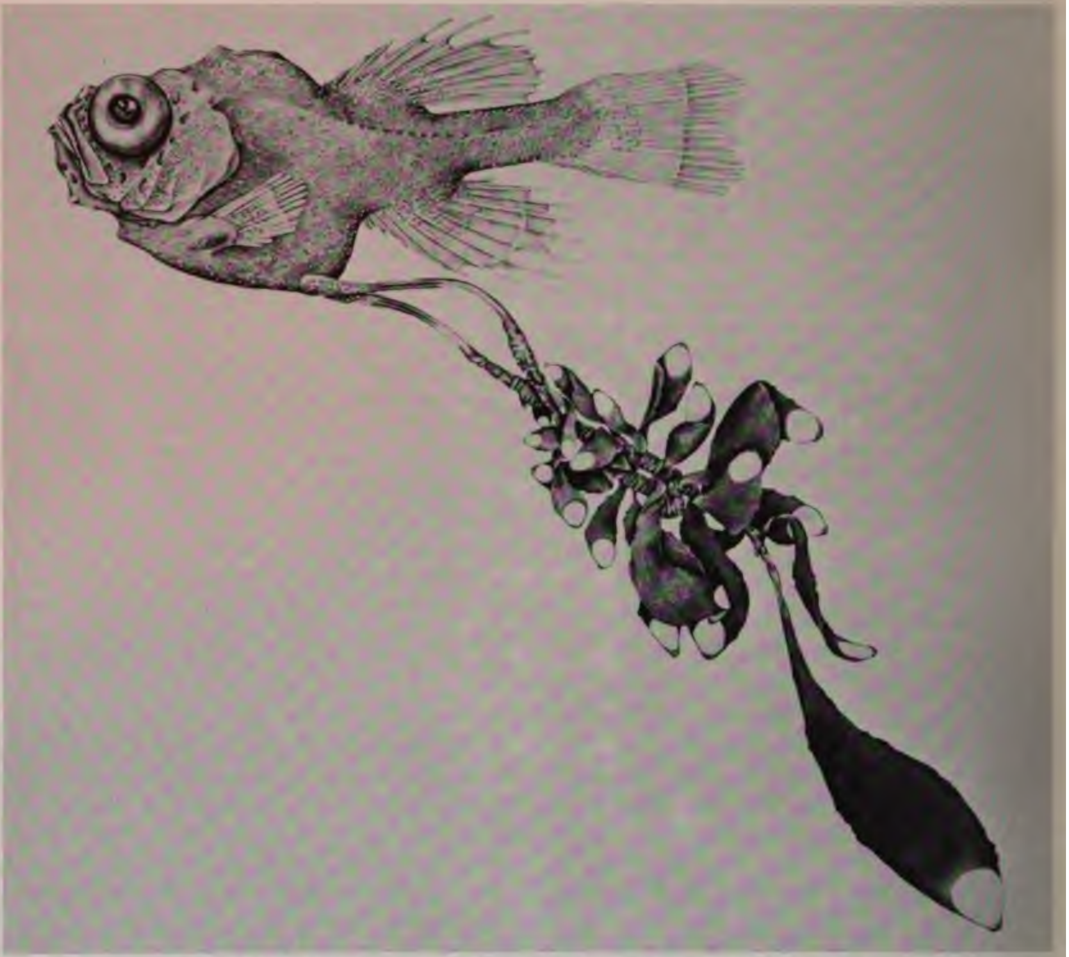

FIGURE 3. *Gibberichthys pumilus*, kasidoron stage, 15.3 mm SL, UMML 28806.

tremely rapid. Other measurements are given in Figs. 8–13.

The most notable changes in body shape, besides proportional differences in eye size, are the shift in position of the mouth from an oblique position to a more terminal one, and a change in the orbit from a sub-superior to a more lateral position. The proliferation of thin, spiniferous crests over the head of the prejuveniles and juveniles is accompanied by closure of the cavernous sulci permeating the head. This transition is observed in the fenestration of the su-

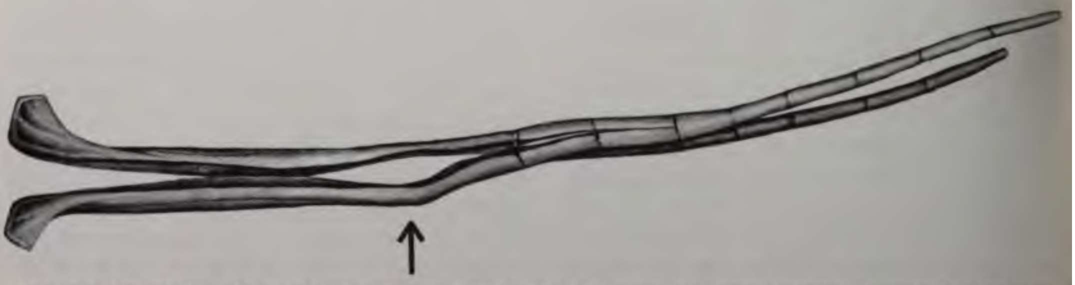

FIGURE 4. Lateral view of the third pelvic fin ray of adult *Gibberichthys pumilus*. Arrow indicates discontinuity (see text).

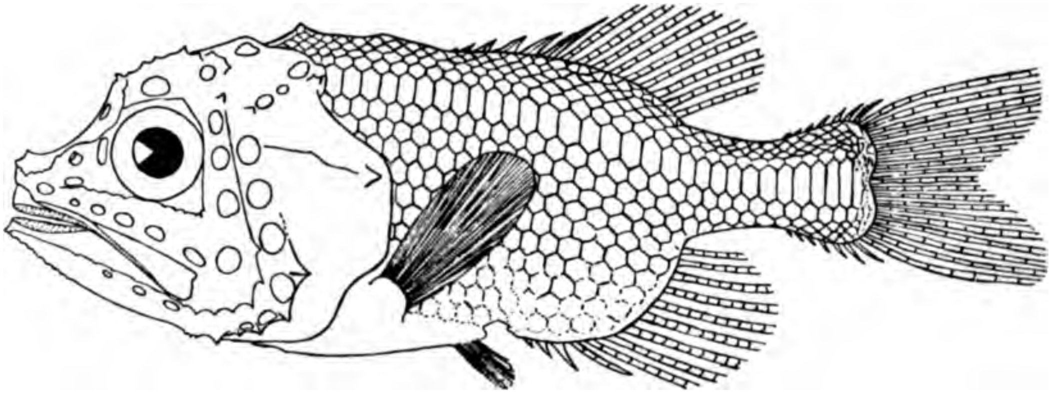

FIGURE 5. Holotype of *Gibberichthys pumilus*, 31.5 mm SL, after Parr, 1933.

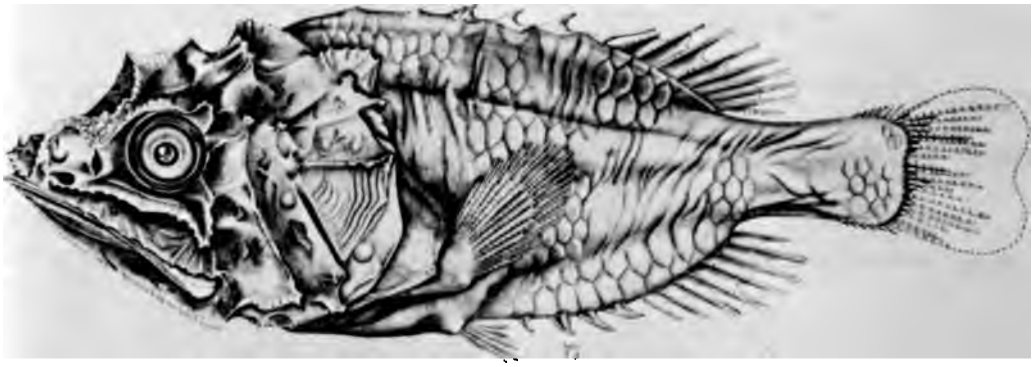

FIGURE 6. *Gibberichthys pumilus*, 82 mm SL, UMML 7041.

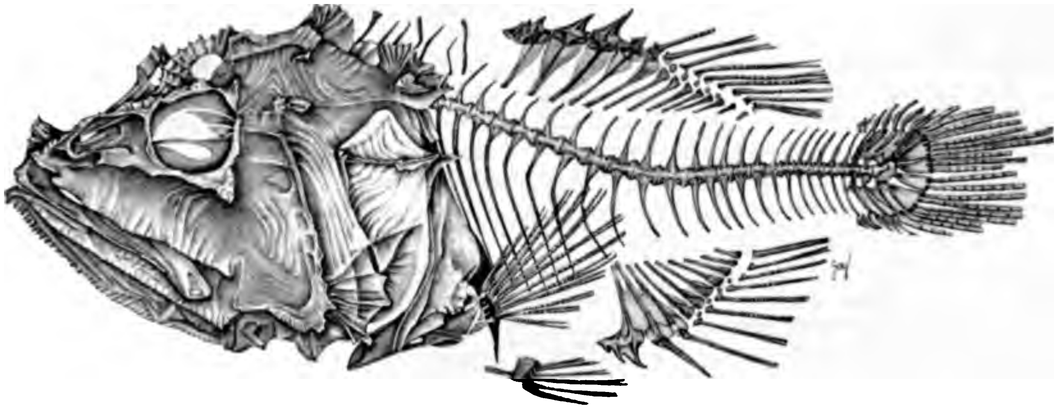

FIGURE 7. *Gibberichthys pumilus*, 87 mm SL, CAS 14564, cleared and stained.

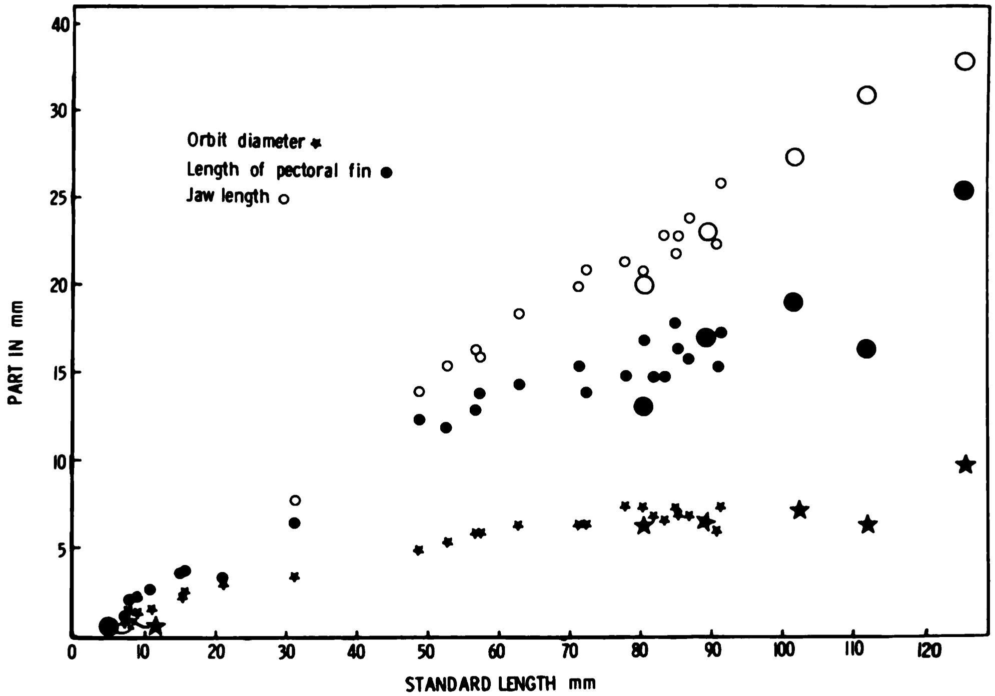

FIGURE 8. Orbit diameter, length of pectoral fin, and jaw length in *Gibberichthys pumilus* and *G. latifrons* (enlarged symbols).

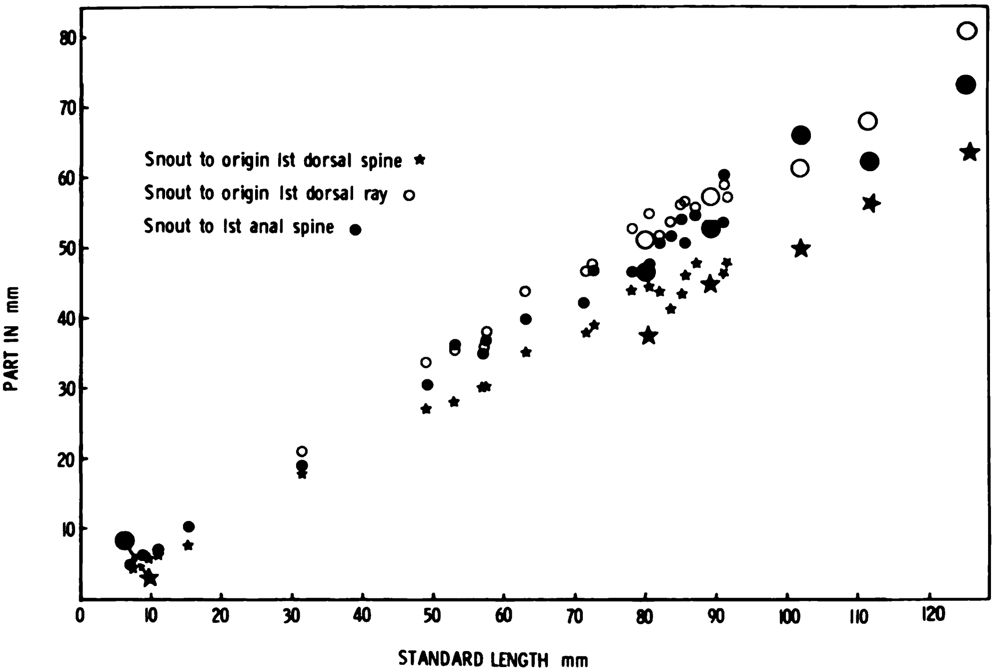

FIGURE 9. Lengths of snout to origin of first dorsal spine, snout to origin of first dorsal soft ray, and snout to origin of first an spine in *Gibberichthys pumilus* and *G. latifrons* (enlarged symbols).

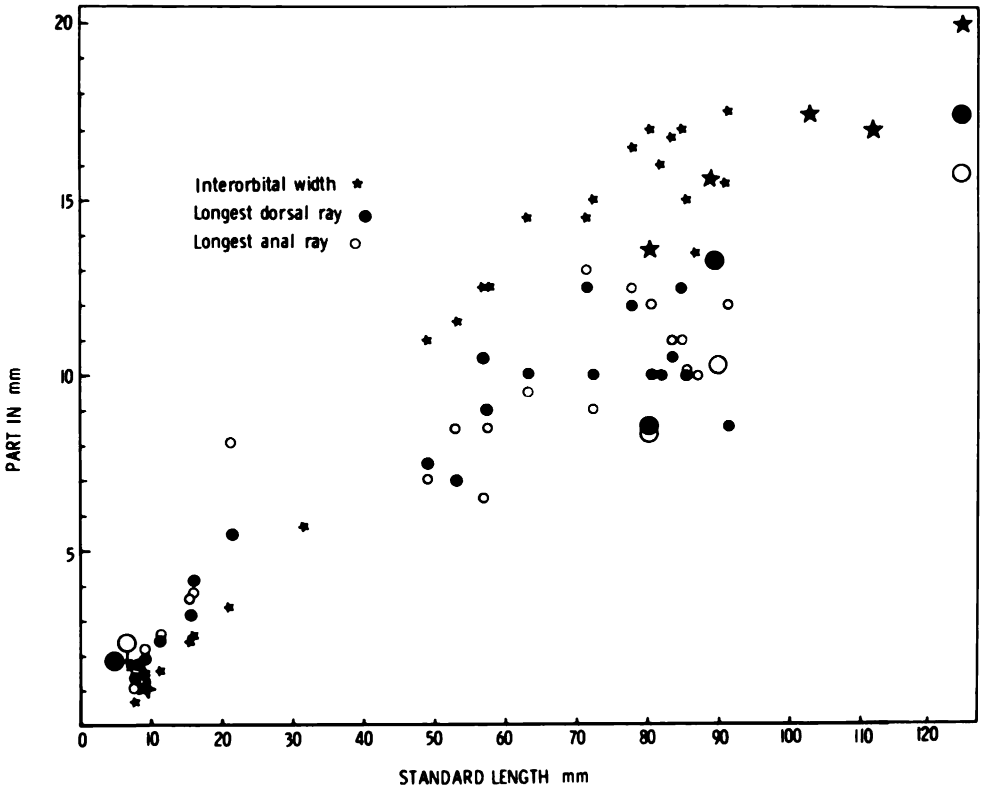

FIGURE 10. Interorbital width, longest dorsal soft ray, and longest anal soft ray in *Gibberichthys pumilus* and *G. latifrons* (enlarged symbols).

praorbital region of a 15.3-mm specimen (Fig. 14a) and is also visible in the same area in adults (Fig. 14b). Similarly, the bony crests so characteristic of the head of adults (Fig. 6–7, 14) are just observable in the internasal region of a 15.3-mm specimen (Fig. 15). As growth continues, the relative position of several cranial bones changes concomitantly to correspond with the lengthening and flattening of the head. These include the change in position of the maxillary to accommodate a rearward shift in the angle of the preopercle and opercle. The maxillary is unsheathed in prejuveniles, but growth of the circumorbital bones partially sheathes the maxillary in larger specimens.

The height of the lumps on the midline behind the head (one character used by Thorp (1969) to distinguish *K. latifrons* from *K. edom*) is due to three interneural (predorsal) bones (see especially Figs. 3, 6–7; see Thorp, 1969, Fig. 1, for *G. latifrons*). Their manifestation as lumps seems more prominent in the prejuveniles than in adults, but this variability may also result from shrinking with preservation.

Little ontogenetic change in coloration occurs; both juveniles and adults are black. The eyes of a freshly captured adult (PILLSBURY sta. 1174) glowed red when a flashlight was shined on them.

Meristic characters.—Counts of dorsal, anal, pelvic, and pectoral rays are similar both in the kasidoron stage and in adults (Table 1). The anterior fin elements in the dorsal and anal fins become spinous when the fish reaches a size between our largest kasidoron stage (21.2 mm) and the holotype of *Gibberichthys pumilus* (31.5 mm). The anterior spines are fixed on broad, firm bases; usually only the last spine is movable. There are usually 6 spinous points in the dorsal fin and 4 in the anal fin. The first plate of the anal fin has 2, while subsequent plates each bears 1 spinous point. Our adult specimens average about 1½ "ray" higher in dorsal "fin-ray" count when spinous points plus soft rays of adults are

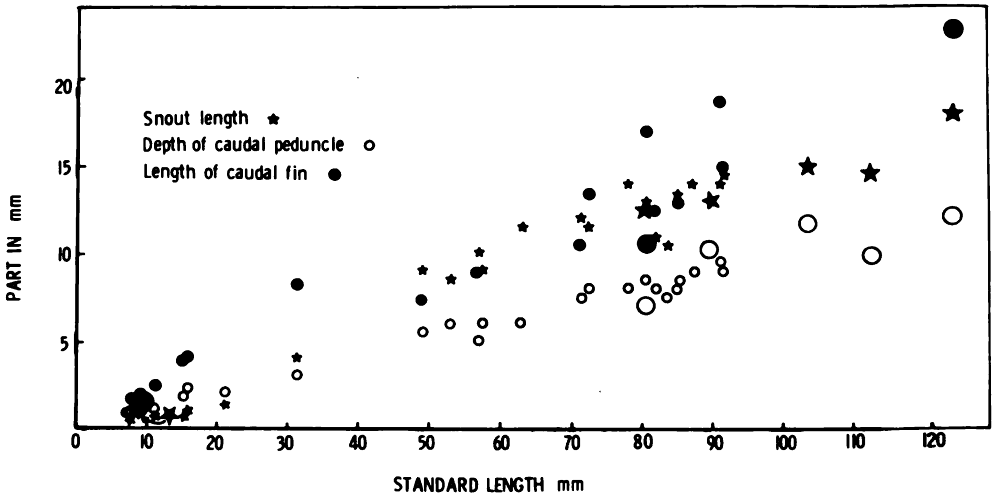

FIGURE 11. Snout length, depth of caudal peduncle, and length of caudal fin in *Gibberichthys pumilus* and *G. latifro* (enlarged symbols).

compared with fin rays of prejuveniles. We believe the first plate of the dorsal and anal fin probably forms from fusion of two fin rays, but usually an extra spinous point develops on the first plate of the dorsal fin which results in the higher dorsal "fin-ray" count of adults. (If three fin rays make up the first plate when it bears three spinous points, then at least one of these elements is not distinguishable in prejuveniles.)

Pelvic rays are usually 6, with the first ray spinous in adults. One specimen, the 7.8-mm paratype of *K. edom*, had only 5 countable pelvic elements, as did one adult. Procurrent caudal rays become spinous after the kasidoron stage; they usually number 7 above and 6 below. Princi pal caudal rays usually number 19, with one ur branched above and one below. The caudal fi structure of an adult is illustrated in Fig. 16.

Vertebrae number 29–30 in three postlarva and 20 adults of *G. pumilus* examined for thi character.

Pyloric caeca.—Pyloric caeca number 12–13 i adult specimens examined for this feature wit about 9 exposed and 3 or 4 under the liver; mos caeca form one whorl, but some caeca lie farthe down the intestine. In the holotype of *K. edon* there were 9 caeca arranged in a single whoı

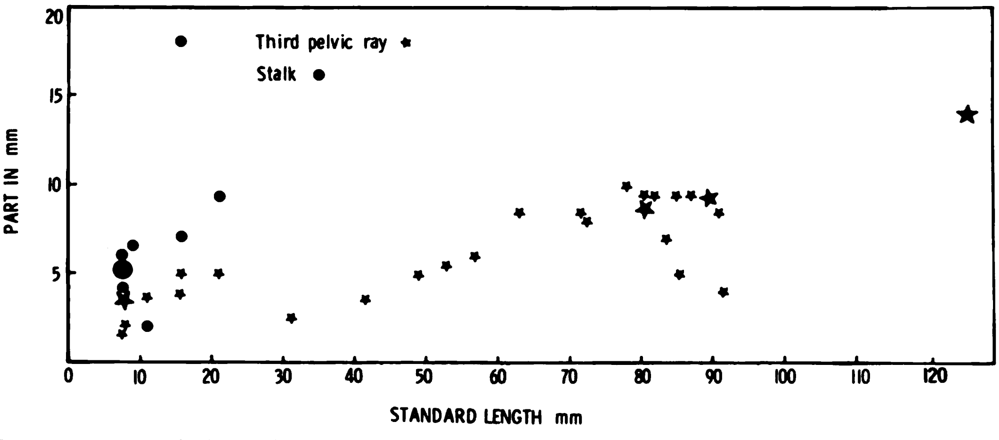

FIGURE 12. Length of third pelvic fin ray and length of the pelvic appendage in *Gibberichthys pumilus* and *G. latifro* (enlarged symbols).

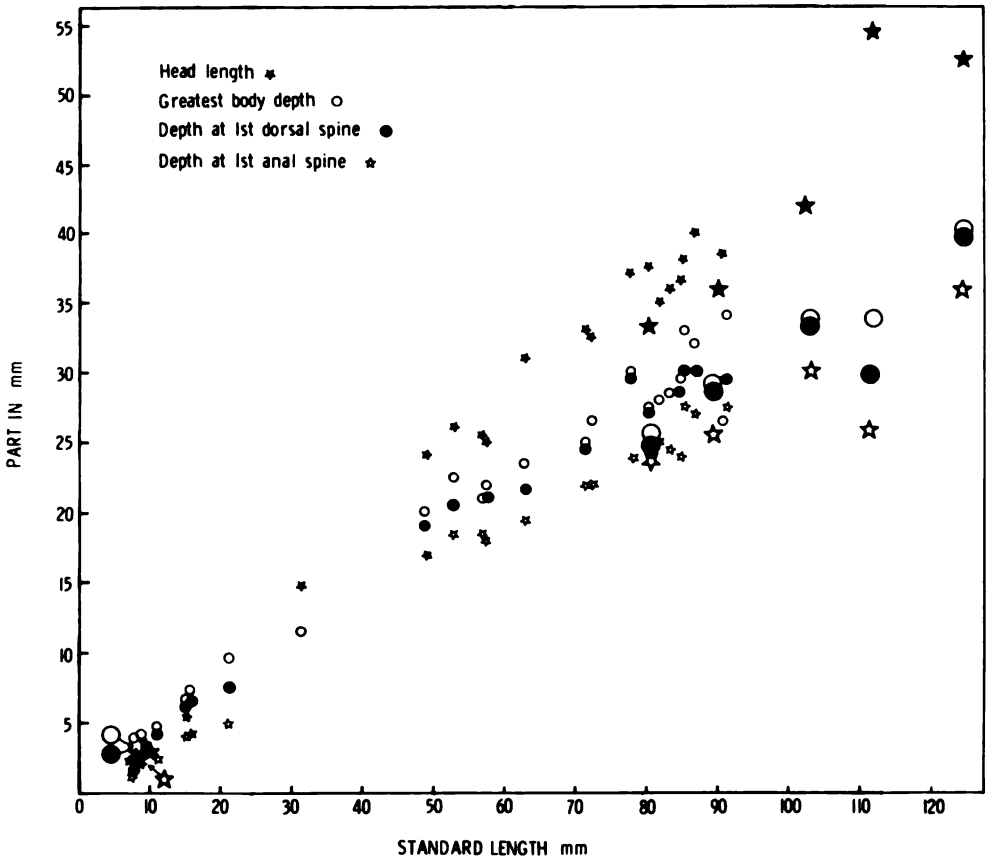

FIGURE 13. Head length, greatest body depth, body depth at origin of first dorsal spine, and body depth at origin of first anal spine in *Gibberichthys pumilus* and *G. latifrons* (enlarged symbols).

(Robins and de Sylva, 1965: 196), but possibly some caeca were rubbed off during examination of this very small specimen, or they were not yet developed. In the prejuvenile specimens and in adults the caeca are pale and long.

Gill rakers.—Counts of gill rakers are particularly difficult to make on the prejuvenile specimens, but the number of rakers on the first arch in these specimens and in adults (Table 1) are comparable. Counts for adults are 5–6 above, one at the angle, and 13–15 on the lower arch, total 18–22 (mean = 20.2, N = 15).

Lateral line.—The lateral line in type specimens of *K. edom* was reported as composed of about 32 vertical rows of raised papillae (Robins and de Sylva 1965: 195). Most skin on the body was rubbed off during caputre of our adult specimens, but in some specimens sufficient skin is intact to permit us to determine that adults also have a lateral line composed of vertical rows of raised pores, each row with about 6 to 8 pores. We are unable to give an exact count of the number of vertical rows, but they are spaced approximately as in the holotype of *K. edom*. Parr (1934: Fig. 37) illustrated the vertical rows of pores and found 28 rows in his 91-mm specimen.

Swimbladder.—Robins and de Sylva (1965: 196) reported that *K. edom* has a well developed swimbladder restricted to the anterior portion of the body cavity. The swimbladder in adult specimens is moderate, thin walled, and lies in the anterior half or two-thirds of the body cavity. It is partially filled with fat in adults.

In summary, differences in the above features can be attributed to ontogenetic changes, features which are the same or nearly so in the small specimens and adults, and those differences

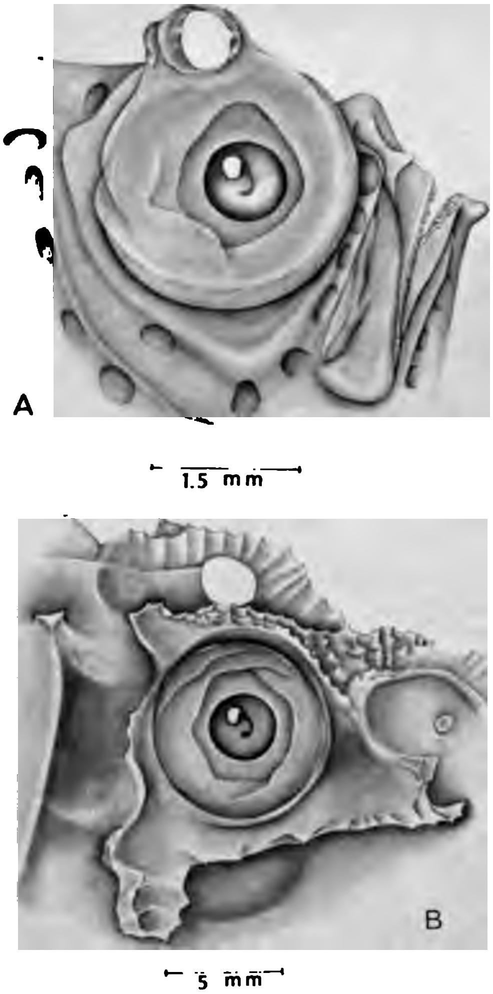

FIGURE 14. Lateral view of oribital region in (A) postlarva, UMML 28806, 15.3 mm SL, and (B) small adult, UMML 7401, 72.5 mm SL, of *Gibberichthys pumilus*.

which may result from error because of the small size of prejuveniles examined. We believe that there can be no doubt that *Kasidoron edom* is the prejuvenile stage of *Gibberichthys pumilus*.

SPECIES OF THE GENUS *GIBBERICHTHYS*

Since *Kasidoron edom* is the prejuvenile of *Gibberichthys pumilus*, then *Kasidoron latifrons* Thorp from the western Indian Ocean is a prejuvenile of the same species or a separate species. We have available only six specimens from outside the Atlantic; Ebeling and Weed (1973) reported one non-Atlantic specimen, and the holotype of *latifrons* brings to eight the total non-Atlantic specimens known.

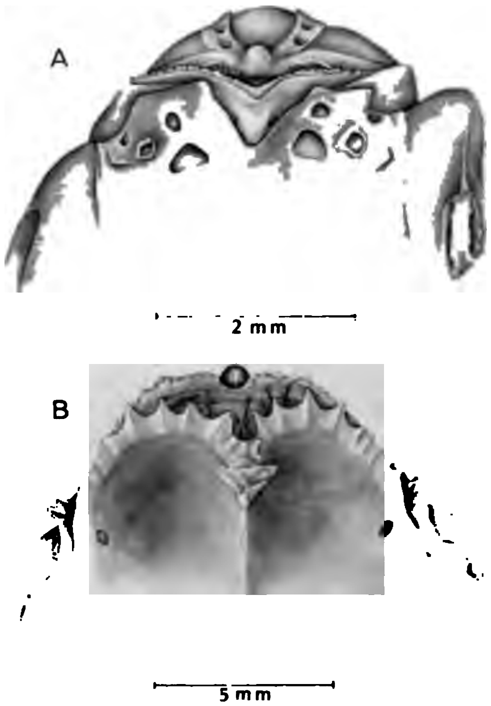

FIGURE 15. Dorsal view of nasal region in (A) postlarva and (B) a small adult of *Gibberichthys pumilus* (same specimens as in Fig. 14).

The differences between the holotype of *latifrons* and prejuveniles of *pumilus* as given by Thorp (1969) are as follows: the lumps behind the head are larger and the body deeper in *latifrons*, and *latifrons* has a minute extra pore in the head lateralis system, no small cycloid scales along the lateral line, a lower gill-raker count, slight differences in measurements, and differences in the pelvic appendage. The dorsal lumps are caused by three interneural (predorsal) bones, and the prominence of the lumps is probably related to some extent by condition or shrinkage with preservation. We are unable to assess the minute extra head pore. The number of gill rakers and other counts (Table 1) fall within the range of *pumilus* based on our material. We are unable to provide much additional information on differences in the pelvic appendage (see Thorp 1969: 68–69) but suspect this to be a structure which is variable in details; no Atlantic prejuvenile has

LE 1. COUNTS FOR SPECIMENS OF *Gibberichthys pumilus* AND *G. latifrons*.

	Dorsal fin rays															
	Prejuveniles				Spinous points + rays in adults							Total (Adults)				
	12	13	14	15	5	6	7	8	+	8	9	13	14	15	16	17
umilus[1]	4	3	1	1	6	9	–	–		5	10	2	7	6	–	–
atifrons[2]	1	–	1	–	–	1	3	1		–	5	–	–	1	3	1

	Anal fin rays												
	Prejuveniles			Spinous points + rays in adults						Total (Adults)			
	10	11	12	4	5	+	7	8	9	11	12	13	14
umilus[1]	2	2	5	13	2		7	7	1	6	7	2	–
atifrons[2]	–	2	–	–	5		2	2	1	–	2	2	1

	Pectoral rays (left side)			Pelvic rays[3] (left side)		Gill rakers[3] (left side)				
	13	14	15	5	6	18	19	20	21	22
umilus[1]	4	16	4	2	21	3	3	6	4	5
atifrons[2]	1	6	–	–	7	1	3	–	–	2

ncludes Parr's (1933) count for one specimen.
ncludes Thorp's (1969) count for holotype.
ome small specimens not included.

arborescence as well developed as Thorp's imen, and the differences in pigmentation of 'leaves" as presented by Thorp may prove to eal differences.

omparison of the five non-Atlantic adults the larger series of Atlantic adults reveals ially no differences between them in counts measurements (see Table 1; Figs. 8–13). Our est specimen of *G. pumilus* is 91.5 mm in dard length while the largest specimen of *G. rons* is 124 mm SL. One major difference was ited out by Dr. John Paxton when he forded the AMS specimen to us. The scales on body appeared to be considerably smaller in specimen from the southwestern Pacific than e specimen figured by Parr (1933). The skin scales are more intact in our non-Atlantic imens and all of the Atlantic adults are missvirtually all scales and much skin. We estie that the scales in Atlantic specimens are t twice the size of scales in the non-Atlantic imens. This difference is easily seen by comng Parr's figure (1933: Fig. 1; reproduced as Fig. 5) and our Figure 6, with the excellent lition of an adult *latifrons* in Ebeling and d (1973: Fig. 12). (Parr's illustration showing w of enlarged scales along the lateral line probably is inaccurate, and we believe that two slightly enlarged scales are present, rather than one enlarged and elongated (vertically) scale, and that both scales house papillae of the lateral line.)

Besides the difference in scale size, the Atlantic and non-Atlantic specimens differ in vertebral counts as given below:

Vertebrae	28	29	30	31
Atlantic specimens	5	18	–	–
Non-Atlantic specimens	–	–	2	3

Because of certain differences in prejuvenile features, and the differences in scale size and number of vertebrae, we recognize two species, *G. pumilus* from the Atlantic and *G. latifrons* from the western Pacific and Indian oceans.

SYNONYMIES

Prior literature may be summarized as follows:

Family GIBBERICHTHYIDAE Parr

Gibberichthyidae Parr, 1933: 1, 4–5 (type-genus *Gibberichthys* Parr, 1933; comparison with other beryciform families). Ebeling 1962: 11 (in Stephanoberyciformes). Ebeling and Weed: 1973. 397 et seq. (relationships). Greenwood et al. 1966: 398 (listed in order Beryciformes, suborder Stephanoberycoidei). Rosen and Patterson 1969: 456, 461

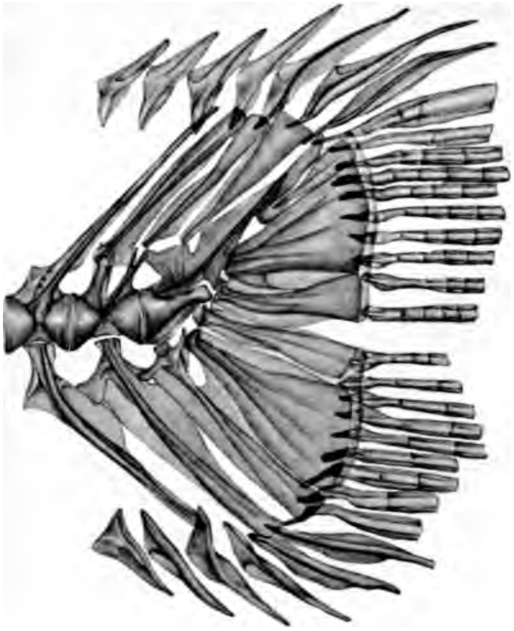

FIGURE 16. Caudal skeleton of *Gibberichthys pumilus*, CAS 14564, 87 mm SL.

(suggested *Kasidoron* was young of *Gibberichthys*; relationships). Rosen 1973: 469 et seq. (relationships).
Kasidoroidae Robins and de Sylva, 1965: 190 et seq. (type-genus *Kasidoron* Robins and de Sylva, 1965). Robins 1966: 696–701 (descriptive information, relationships).
Kasidoridae (*sic*), Myers and Freihofer 1966: 193–194 (compared with Megalomycteridae). Greenwood et al. 1966: 395 (listed in suborder Mirapinnatoidei, order Cetomimiformes).

Genus **Gibberichthys** Parr

Gibberichthys Parr, 1933: 5 (type-species *Gibberichthys pumilus* Parr, by original designation, monotypic).
Kasidoron Robins and de Sylva, 1965: 190 (type-species *Kasidoron edom*, by original designation, monotypic).

Gibberichthys pumilus Parr

Gibberichthys pumilus Parr, 1933: 5–6, Fig. 1 (type-locality 21°44′N, 72°43′25″W, 2134 m wire, 6 Apr. 1927, PAWNEE sta. 48: BOC 2838). Parr 1934: 35–36, Fig. 11 (description of 91-mm specimen; ATLANTIS sta. 1478; compared with holotype). Myers 1936: 118 (belongs near Stephanoberycidae). Springer and Bullis 1956: 66 (listed; Gulf of Mexico, OREGON sta. 1425). Grey 1959: 333–334 (description of a 47-mm specimen, 29°04′N, 88°05′W, 914 m, OREGON sta. 1425). Ebeling and Weed 1973: 412–414 (in part; figure and part of description is *G. latifrons*; family relationships).
Gibberichtys pumilus, Ebeling 1962: 11 (misspelled genus; agreed with Rofen that it was allied to melamphaeids).
Kasidoron edom Robins and de Sylva, 1965: 189 et seq., Figs. 1–2 (original description; types from near Bermuda and NE of Bahamas). Robins 1966: 696 et seq., Figs. 1–3 (additional information on *K. edom*; relationships). Voss and Sisson 1967: 393 (figure). Thorp 1969: 62 et seq. (compared latifrons). Rass 1971: plate opposite p. 97 (figure; pelvic appendage shown as luminescent).

Gibberichthys latifrons Thorp

Gibberichthys latifrons Thorp, 1969: 61–70, Figs. 1–4 (description; type-locality near Zanzibar, 08°34′S, 4 good description; compared with *K. edom*).
Gibberichthys pumilus, Ebeling and Weed 1973: 412–4 12 (good figure; did not distinguish *latifrons* from e

Distribution and Biology

Gibberichthys pumilus is now known several localities in the western Atlantic (Fi *Gibberichthys latifrons* is known from the ern Indian Ocean (3 specimens), the Haln Sea area (3), near Samoa (Ebeling and 1973) (1), and west of the Marquesas Islan We attribute the separate distribution o juveniles and adults in the Atlantic Ocea 17) to an artifact of collecting methods and The prejuveniles were captured in oceanic where University of Miami PILLSBURY tions were concentrated, and most adult caught in coastal waters where OREGO OREGON II trawling operations were cond We expect the species is widespread in the ern Atlantic.

Lack of data from closing nets allows u limited interpretation of the vertical distri of adults. The prejuveniles are epipelagic, a tures being taken between near-surface and about 50 m. All captures were made a and no specimens were taken in near-surfac light tows. One might infer from the black ation of the fish that prejuveniles may u diel migration at least into lower epipela upper mesopelagic levels during daylight Changes in morphology between the preju stage and the juvenile stage, which occur at the time that the fish descend into the mesopelagic or upper bathypelagic level discussed in an earlier section.

Capture of adults has been by use of bo tom trawls and midwater nets. The shall bottom trawl haul in the western Atlantic 320 m and the deepest in 841 m, with most range of 650–750 m. Additional collecti adults from vertical tows and non-closing n ter nets add limited information; one captu estimated to be at 800–1100 m and another i or 1100 m. It would appear that the depth ra adults in the western Atlantic is roughly fr

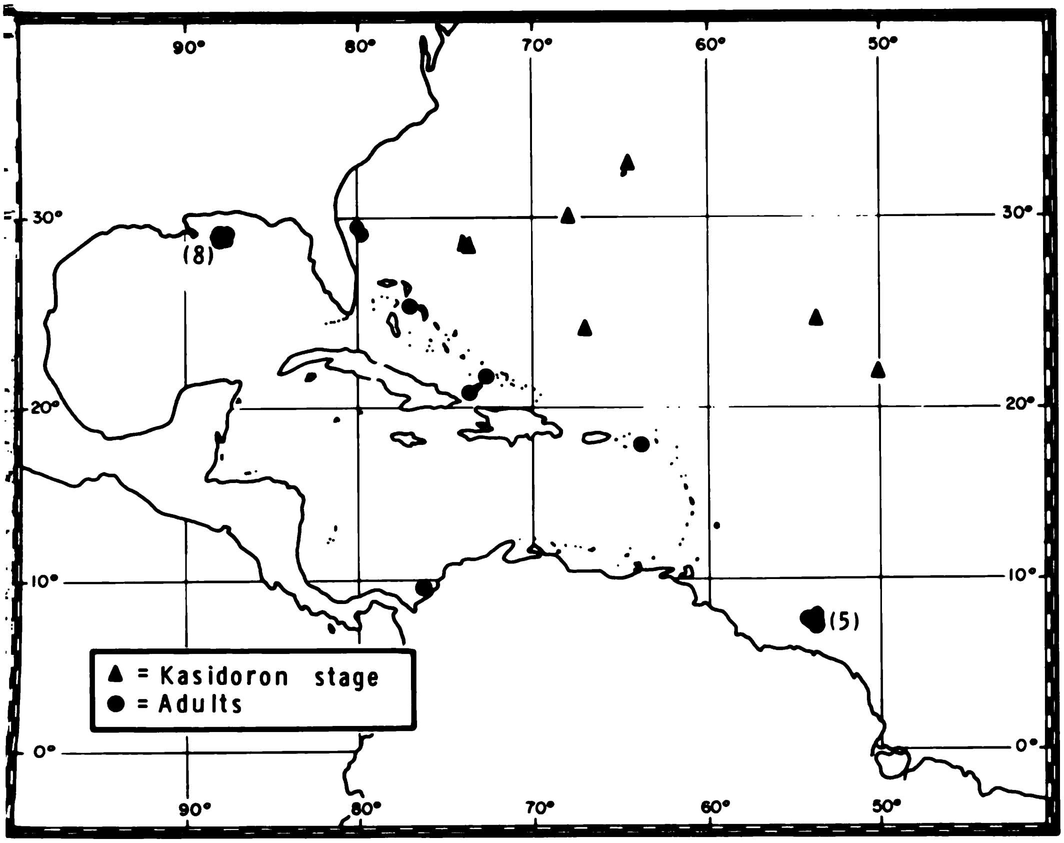

FIGURE 17. Distribution of *Gibberichthys pumilus* in the western Atlantic Ocean (symbols represent stations).

to 1000 m; however, one adult of *latifrons* from e western Indian Ocean was collected at a epth of 58 m (correspondence with Leslie napp indicates that the depth of capture is accute). The adult from the southwestern Pacific as from an oblique tow between 0 and 1040 m, nd the one reported by Ebeling and Weed (1973) etween 0 and 1000 m. The presence of fat in wimbladders of adults and the absence of capures in near-surface waters at night, where ost trawl hauls for midwater fishes have been ade, suggests that adults do not undergo vercal migration, at least not into near-surface aters.

The food of postlarval specimens was reported y Robins and de Sylva (1965: 200) as copepods, articularly calanoid copepods. Stomachs of 16 dults of *Gibberichthys pumilus* were removed nd the contents examined. Fifteen specimens ontained food, 13 of which had identifiable conents as follows:

Category	Number of stomachs in which organism was found
Amphipoda	
Gammaridea	
Lysianassidae	
Cyphocaris johnsoni	11
Hyperiidea	
Hyperiopsidae	
Hyperiopsis sp.	1
Copepoda	
Calanoida	
Eucalanidae	
Eucalanus elongatus	1
Metridiidae	
Pleuromamma abdominalis	1
Harpacticoida	1

The pelagic gammaridean *Cyphocaris johnsoni* was by far the most common food of adults, occurring in 11 stomachs, usually from 1 to 8 per stomach. Nearly all stomachs contained crustacean fragments, usually of amphipods. According to Vinogradov (1970: 209) the pelagic gammarids in the total plankton mass above 3000 m is negligible, but since these amphipods were common in stomachs and because other plankters were few, we suspect that *Gibberichthys pumilus* is selective in its food habits.

The use of the pelvic appendage deserves additional study. Robins and de Sylva (1965: 199) reported on the swimming behavior of a freshly captured specimen in a shipboard aquarium. They suggested that the pelvic appendage may mimic the nectosome of siphonophores. A more complete description of the pelvic appendage was given by Robins (1966: 698–700), particularly regarding microstructure. No sign of any specialized structure that could account for luminescence was found, and no muscle fibers or nerves were found associated with the stalk or "leaves." However, the epithelium on the tips of the pelvic appendage had been sloughed off in the specimen examined by Robins and de Sylva (1965) (personal communication from Mrs. Priscilla Rasquin Breder), so that epithelial luminescent structures could have been lost. A second specimen was observed alive by de Sylva (PILLSBURY sta. P-1053). The specimen lived for about four hours, swam only moderately, alternating bursts of active swimming near the surface with periods of quiet on the bottom. Its behavior appeared abnormal. Periodic examination of the specimen in the dark showed that the "leaf" tips, if luminescent, were not noticeably so, but the room was not completely dark. The tips of the fresh "leaves" were pale greenish yellow, a cast sometimes characteristic of luminous structures (see Nicol 1967, 1969). A color illustration which shows the presumed luminous nature of the epithelium of the tips is presented in Rass (1971: plate opposite p. 97). The simple nature of the pelvic appendage would seem to rule out voluntary control of the luminescence, but bacterial associations might be possible. (However, we would caution against illustrations depicting luminescence [e.g., Rass 1971] because it is quite possible that no luminescence is involved.) The apparent lack of muscles associated with the pelvic appendage renders it passive and would seem to limit its use to either mimicry as proposed by Robins and de Sylva (1965) or general deception, particularly when viewed from below or behind, or as a "cover" source which might attract food items. The arborescence in Thorp's specimen (1969: Fig. 1) resembles *Sargassum* weed more than in Robins' specimen (1966: Fig. 1).

Ripe gonads were found in two femal
mens measuring 81 and 87 mm SL coll
May 10th. The eggs contain an oil globul
is no evidence that the species is hermap

REMARKS

The relationships of the famil
berichthyidae deserve additional stu
agree with Ebeling and Weed (1973) that
ily Gibberichthyidae seems to show clos
tionships to the family Stephanoberycid
more distant relationship to the Melamp
A brief examination of stephanobery
melamphaeids was made, and we found
cation that a prejuvenile pelvic appenda
in any xenoberyciform group exce
berichthys. Some melamphaeids, pa
postlarval specimens of the genus *Po*
have extremely long pelvic fins with
vidual rays branched many times and b
hair-like distally. The family Gibbericht
uniquely characterized by the presenc
pelvic appendage in postlarval specime
separated by Norman (1957: 213) from
phaeids and stephanoberycids on the ba
presence of spines in the pelvic, dorsal,
fins in *Gibberichthys*, especially the rig
with broad, flattened basal plates in t
and anal fins (see also Ebeling and We
When one recalls that the soft fin ra
kasidoron stage become the fin spines
berichthys, it is not difficult to consider t
lar transitions of rays to fin spines may al
in other groups of deep-sea fishes which
pected of bizarre metamorphoses.

We also briefly examined specimens
deletia bicolor and were struck by
semblance of this fish to *Gibberichthys*
Rofen (see Ebeling 1962: 11; Ebeling a
1973: 399). Ebeling and Weed (1973:
cussed the problems surrounding pl
of *Rondeletia* and the classification
groups, their orders Xenoberyces (S
beryciformes), Beryciformes, and C
(Cetomimiformes). Add to this the f
Robins (1966) placed the postlarval *K*
edom in the Mirapinniformes. In turn h
these near the Cetomimiformes, an
that some of them were prejuveniles
mimids (Robins 1974), e.g. *Megalomyct*
olepis (C. R. Robins, personal com
tion). However, Rosen and Patterson (
moved *Kasidoron* to the Beryciformes (

Cetomimoidei) but did not comment on
ainder of the mirapinniform fishes except
de them (op. cit.: 461) in the Lam-
mes. Nor does the reshuffling and reor-
; of these groups by Rosen and Patterson
om the classification of Greenwood et al.
dvance our understanding of relation-
cept to move the Lampridiformes next to
yciformes and place all of them in the
perorder. Rosen (1973) has further re-
these and other groups and presented
: 469) a working hypothesis that there is a
iv) within a broad order Beryciformes
ng the Barbourisiidae, Rondeletiidae,
chthyidae, Cetomimidae, Mirapinnidae,
ophoridae, Megalomycteridae, Melam-
e, Stephanoberycidae, and Anoplogas-
It is apparent that the higher-category
ation of these fishes remains uncertain.
nt collections of deep-water fishes by
searchers are disclosing that our knowl-
metamorphosis of deep-water fishes is
known, and bizarre transformations in-
more than one metamorphosis may be
n in certain fish groups. Certainly, the
of such groups as the Rosauridae,
mycteridae, Mirapinnidae, and Eutae-
idae should be re-examined, and some
g studied by other workers. It is possible
east some of these represent prejuvenile
f cetomimoid, berycoid, or other fishes.

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OF THE

CALIFORNIA ACADEMY OF SCIENCES

FOURTH SERIES

Vol. XLI, No. 7, pp. 233–251; 11 figs.; 5 tables August 18, 1977

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20 1977
CURRENT SERIAL SERVICE

A NEW GENUS (*MESOBIUS*), AND THREE NEW BATHYPELAGIC SPECIES OF MACROURIDAE (PISCES, GADIFORMES) FROM THE PACIFIC OCEAN

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ABSTRACT: A new genus, *Mesobius*, and three new species (*M. berryi, M. antipodum, Nezumia parini*) of bathypelagic macrourid fishes are described from the Pacific Ocean. *M. berryi* is known from the eastern North Pacific, *M. antipodum* from a single adult off New Zealand, and *N. parini* from the equatorial eastern Pacific and midwaters between Panama and northern Chile. *M. berryi* passes through a phalacromacrurus stage characterized in early prejuveniles by bold spotting on the head and body, stylopterus pectorals, and almost vertical jaws. Later prejuveniles have normal pectorals and more nearly horizontal mouths. Spots remain on the trunk and tail in individuals as large as 40 mm in head length, but the general blackish color characteristic of all bathypelagic macrourids obtains in older individuals. The small jaw teeth in narrow bands, the uniquely elongated and aligned head scales, and the seven branchiostegal rays of *Mesobius* contrast with the fanglike teeth in single series, the circular head scales, and the six branchiostegal rays of two other bathypelagic macrourids, *Odontomacrurus murrayi* and *Cynomacrurus piriei*. It appears to be most closely related to the monotypic genus *Echinomacrurus*. *Nezumia parini*, the only known bathypelagic member of an otherwise exclusively benthopelagic genus, retains many of the characters of its benthopelagic relatives, but it has the reduced musculature, skeleton, gill-filaments and gas-bladder of other bathypelagic macrourids. Its small scales are distinctively covered with very fine, erect spinules, that yield a velvety texture to body surface.

INTRODUCTION

Most of the 250 or so species of the deepsea fish family Macrouridae are benthopelagic as adults. These benthopelagic species generally hover and glide over the bottom at an inclined, nose-downward attitude while seeking out their bottom-dwelling or near-bottom prey. Those that have become restricted to feeding on food items buried within the bottom substratum tend to have a small, protrusible, inferior mouth and a strongly reinforced spade-shaped rostrum that aids in rooting out prey. The more generalized feeders tend to have a larger, more terminal mouth. Many of those that feed on fish, cephalopods, and swimming crustaceans are known to seek their prey well off bottom. Examination of stomach contents of the abyssal species *Coryphaenoides armatus* Hector, 1875, *C. leptolepis* Günther, 1877, and *C. filifer* (Gilbert, 1895) has revealed a high proportion of

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pelagic food items in their diet (Pearcy and Ambler 1974; Haedrich and Henderson 1974). Dense aggregations of *Coryphaenoides rupestris* (Gunner, 1765) are known to rise regularly to 100–300 m off bottom in the western North Atlantic (Pechenik and Troyanovskii 1970; Haedrich 1974). *Coryphaenoides acrolepis* (Bean, 1884), a species of the North Pacific, though primarily benthopelagic, has also been reported captured thousands of meters above bottom (Rass 1963:221; Makushok 1967:201; Iwamoto and Stein 1974:16). The bizarre, globose-headed species *Squalogadus modificatus* Gilbert and Hubbs, 1916, *Macrouroides inflaticeps* Smith and Radcliffe, 1912, and *Echinomacrurus mollis* Roule, 1916, are probably primarily bathypelagic, but they have been taken most often in bottom trawls.

Most species of macrourids probably dwell at bathypelagic or mesopelagic depths as larvae or juveniles (Marshall 1965). A few species have adopted, as adults, an exclusively pelagic habit in the deep midwaters of the oceans. When he reviewed the bathypelagic macrourid fishes, Marshall (1964) considered only two species, *Odontomacrurus murrayi* Norman, 1939, and *Cynomacrurus piriei* Dollo, 1909, as being strictly confined to the midwaters of the ocean, although he suspected (and later, with Tåning (1966), gave evidence) that *Macrouroides inflaticeps* Smith and Radcliffe and *Squalogadus modificatus* Gilbert and Hubbs were probably primarily bathypelagic. *O. murrayi* is known mostly from the eastern Atlantic, although the holotype was taken in the Indian Ocean. *C. piriei* is known only from waters inside the Antarctic Convergence, where it abounds.

In the present paper, we describe three new species of bathypelagic macrourids, all from the Pacific. Two are clearly referable to a trenchantly distinct new genus, *Mesobius*. The third is referred to *Nezumia*, a genus of numerous, almost exclusively benthopelagic, species. The three new species are known only from captures made in midwater nets fished far off the bottom.

METHODS

Methods for taking measurements and counts generally follow procedures outlined by Hubbs and Lagler (1958), but are modified for macrourids as indicated by Gilbert and Hubbs (1916) and Iwamoto (1970).

Proportional measurements are not given as
the customary percentages of the s
length, because of the usual greater or le
and abrupt regeneration of the caudal tip
a pseudocaudal fin. In place of following
and Hubbs (1916) in using as a meas
base the length from snout tip to anus (
highly variable due to the frequent di
caused by the dorsal flexure of the head
become common to employ as the base t
length, from the extreme tip of the sno
most posterior bony margin of the ope

In the Material Examined sectio
museum catalog number for each lot is f
in parentheses, by the number of speci
their ranges of head length and total len
cality and capture data complete the inf
for each lot. Depths, when originally
fathoms, have been converted to the ne
ter. Abbreviations generally follo
suggested in "The Council of Biology
Style Manual" (American Institute of B
Sciences 1972). Others used includ
cruise; HL—head length; IKMT—Isa
midwater trawl; m.w.o.—meters of wi
towing warp); R/V—research vessel
station; TL—total length.

Museum abbreviations are as
CAS—California Academy of Scien
Francisco, California; FAKU—Facult
riculture, Kyoto University, Maizuru
LACM—Museum of Natural History
Angeles County, California; PPSIO—P
shov Institute of Oceanology, Academ
ences USSR, Moscow; SIO—Scripps I
of Oceanography, University of Califo
Diego, La Jolla, California; USNM—
Museum of Natural History, Smiths
stitution, Washington, D.C.; VIMS—
Institute of Marine Science, Gloucester
ginia; ZMUC—Zoological Museum, U
of Copenhagen.

ACKNOWLEDGMENTS

We thank the many persons, who, i
ways, have helped us in the completio
paper. The following provided or help
loan of specimens: E. H. Ahlstrom a
Moser (National Marine Fisheries
(NMFS), La Jolla, California); M. A.
(SIO); F. H. Berry (NMFS, Miami, Fl
M. Clarke (University of Hawaii);
manoir (ORSTOM, Noumea); K. Fujit
University of Fisheries); A. Fleminger (

(Smithsonian Oceanographic Sorting
'ashington, D.C.); K. Kuronuma (To-
. Lavenberg (LACM); K. F. Liem and
an (Museum of Comparative Zoology,
D. F. Markle (VIMS); I. Nakamura
J. Nielsen (ZMUC); N. V. Parin
R. H. Rosenblatt (SIO); and P. J.
r (NMFS, Honolulu).

:ch, California Department of Fish and
ɔng Beach, California, provided the
in Figure 3 along with information on
ıs of *Mesobius berryi*.

ffrey Moser very kindly and skillfully
us the early prejuvenile of *Mesobius*
;. 6). Other illustrations were drawn by
ith (Fig. 11), C. Pape (Figs. 2 & 4).
ures, 5, 7, 8, 10, were drawn by T.
) Radiographs were made by J. E.

ir critical review of the manuscript we
liam N. Eschmeyer, N. B. Marshall,
ırd H. Rosenblatt.

us Hubbs and Iwamoto, new genus

PECIES.—*Mesobius berryi* Hubbs and

ɔsıs.—The two species of the genus are
gic. Each has seven branchiostegal
anus and the urogenital opening are
:d by a raised margin of black naked
hus are removed from the origin of the
ı the width of that margin. A large light
ng anterior to the anus, abuts the an-
l of the rectum (Fig. 5). The anus, the
ɜ, and anal-fin origin are displaced far
ɔn the short abdomen; the distance
isthmus to the anal-fin origin slightly
he interorbital width, and is less than
ɜ the postorbital length. The mental
ıbsent. The sensory pores of the head
and inconspicuous. The dentition in
ɜr and lower jaws comprises narrow
small depressible teeth, with none en-
ıe upper-jaw tooth bands are widely
at the symphysis. The body scales
are small and thin. Those near the dor-
ntral margins of the trunk and tail bear
, erect spinules on the exposed field;
ıe scales along the flanks lack spinules.
s on the head (Fig. 4B) are uniquely
; each bears 1–3 rows of spinules that
, sharp ridges with 2–9 spinules per
head and body are compressed. The eyes of adults are only moderately enlarged (orbit diameter 23–31 percent of head length). The mouth is large (upper-jaw length 40–47 percent). The gill-membranes are narrowly attached to the isthmus and have a narrow posterior free fold. The wide opercular opening extends anteroventrally to a vertical about one corneal diameter behind the orbit. The first (outer) gill-slit is restricted. The greatly reduced gas-bladder bears two retia and two gas glands. Some of the short caeca are bifid at the base. Postlarvae and prejuveniles pass through a polka-dotted ("phalacromacrurus") stage; adults are mostly black. Styloptery (referring to the stalked pectoral fins) of the postlarvae is extreme, reminiscent of the stylophthalmy (greatly stalked eyes) of the postlarvae of *Idiacanthus*.

RELATIONSHIPS.—*Mesobius* is referable to that group of macrourine rattails that has in common the combination of seven branchiostegal rays and the anus only slightly removed from the anal fin by the width of a broad, circumanal margin of naked black skin. Related genera include *Echinomacrurus* Roule, *Trachonurus* Goode and Bean, *Cetonurus* Günther, *Paracetonurus* Marshall, and *Sphagemacrurus* Fowler. Of these genera, *Mesobius* seems closest to *Echinomacrurus*, a monotypic genus of the eastern North Atlantic and western Indian Ocean (Marshall 1973:600).

These two genera are similar principally in having a relatively short trunk (with pelvic and anal fins and anus far forward), much reduced or lacking gas-bladder, black coloration, reduced or absent chin barbel, and small teeth in narrow bands in each jaw. These characters, however, may reflect convergent life styles rather than phylogenetic proximity. The degree to which each character is developed in *Mesobius* and *Echinomacrurus* as a specialization to a bathypelagic habit is generally the more extreme in *Mesobius*, a strictly bathypelagic fish, and less modified in *Echinomacrurus*, a sometime dweller of the bathypelagic realm. Interestingly, however, the gas-bladder is entirely lacking in *Echinomacrurus* (Marshall 1973:509), but is only regressed in *Mesobius* (a condition that one might not expect). In the two other bathypelagic genera, *Cynomacrurus* Dollo and *Odontomacrurus* Norman, the gas-bladder is also regressed (Marshall 1964). Significantly, all of these bathypelagic genera have weakly ossified skeletons.

Aside from the characters mentioned above (and until the internal morphology of both genera has been more closely compared), there appear to be few characters that would indicate close relationship between *Echinomacrurus* and *Mesobius*. The differences between the two genera are more obvious. Whereas *Mesobius* has a compressed head with only a moderate development of mucous chambers, in *Echinomacrurus* the head is broad and inflated, "due mainly to the very wide lateralis canals" (Marshall 1973:598). The mouth of *Mesobius* is large and almost terminal, whereas that of *Echinomacrurus* is small and inferior. The greatly elongate and closely seriated head scales of *Mesobius* contrast sharply with the small, round, non-imbricate scales of *Echinomacrurus*.

Mesobius is far removed from three other strictly bathypelagic macrourids: *Odontomacrurus murrayi*, *Cynomacrurus piriei* and *Nezumia parini* Hubbs and Iwamoto. *Odontomacrurus* and *Cynomacrurus* each has six branchiostegal rays, large fanglike, jaw teeth, and large open sensory pores on the head. *Mesobius*, in contrast, has seven branchiostegal rays, small teeth in a narrow band in the jaws, and no apparent open sensory pores on the head. *Nezumia parini*, like *Mesobius*, has seven branchiostegal rays and a light organ closely associated with the anus, but the position of the periproct (distantly removed from anal fin and closer to pelvic fins), the presence of a strong suborbital ridge and a stout terminal snout scute, the relatively small, inferior mouth, and the restricted gill membranes, all indicate that *Nezumia parini* is a member of a phylogenetic line very divergent from that of *Mesobius*. It appears then, that the bathypelagic macrourids have had a diverse origin, and that they are not from one evolutionary line but from several.

DISTRIBUTION.—From our study material, the genus appears to be confined to the Pacific Ocean—*M. berryi* to the northeastern portion and *M. antipodum* to the southwestern portion. Dr. N. B. Marshall, however, writes (*in litt.*, 17 March 1976) of having found a young *Mesobius* in the DANA collection (sta. 1166 IV, 10°16'N, 40°41'W), and that he now believes that the polka-dotted young reported by Backus *et al.* (1965) as *Sphagemacrurus*? is also a *Mesobius*. He concludes: "I expect that *Mesobius* has a world-wide distribution between the subtropical convergences."

TABLE 1. FREQUENCY DISTRIBUTIONS OF SELECTED COUN OF *Mesobius berryi* HUBBS AND IWAMOTO. ABBREVIATIO FIRST DORSAL FIN—1D.; PECTORAL FIN—1P.; PELVIC FIN 2P; GILL-RAKERS ON MEDIAL ROW OF FIRST ARCH—GR GILL-RAKERS ON MEDIAL ROW OF SECOND ARCH—GR II.

	7	8	9	10	11	12	13	14	$\bar{x}$
1D.				3	9	3			11.00
1P.*						3	21	5	13.07
2P.*	11	17	2						7.70
GR I				1	4	7	3		11.80
GR II				2	11	2			11.00

* Includes counts of both right and left fins from eac specimen.

ETYMOLOGY.—The name *Mesobius* is derive from μεσος (mesos), middle, and βιος (bios) life, referring to the bathypelagic habitat of th genus.

Mesobius berryi Hubbs and Iwamoto, new species

(FIGURES 1–8, 10A; TABLES 1–3)

"Macrouridae, unidentified" Berry and Perkins 1966:66 ("an undescribed genus and species of bathypelagic macrouroid"; two specimens from R/V COBB, cr. C6303, sta 86.92, 305 km SW of Point Conception, California, in approximately 640 m.)

DIAGNOSIS.—A species of the genus *Mesobiu* with 12–17 pyloric caeca; medial gill-rakers o first arch 10–13, on second arch 10–12; snou length 23–28 percent and interorbital widt 28–34 percent of head length.

DESCRIPTION OF ADULTS.—Selected count are given in Table 1 and measurements in Tabl 2.

General Adult Features: The general adul features of this unique fish may be seen in th illustration of the holotype (Fig. 1). The hea and body are compressed; the greatest width o the head is about half the greatest body depth The fin rays are fragile and slender, and th skeleton is poorly ossified. Most of the derma head bones are thin, in part almost membranous The integument of the head and body is thin, bu is not membranous (as it is in members of th genus *Hymenocephalus*). The temporal regio of the head is much enlarged. The high supraoccipital crest forms a distinct arch in the dorsa profile. Ventral aspects of the abdomen ar short; the distance from the isthmus to the ana fin is about 1.0 1.5 orbit diameters. The anus pelvic fins, and anal-fin origin are displace

TABLE 2. SELECTED MEASUREMENTS FROM 15 TYPE-SPECIMENS OF *Mesobius berryi*. TOTAL LENGTH AND HEAD LENGTH IN MILLIMETERS; OTHERS IN THOUSANDTHS OF HEAD LENGTH.

	LACM 35671	SIO H51–87	LACM 30083–17	LACM 8638	CAS 30469	USNM 215326	CAS 30471	SIO 73–170	CAS 30470	USNM 215326	SIO 72–374	SIO 73–327	USNM 215327	USNM 215327	LACM 9579–16
Total length	165	182	190	170	257	307	340	344	316	345	358	397	333	374	392
Head length	15.7	16.7	26	33	49	57	61	61.8	62	62	64	65	65.8	68.9	70
Postrostral length	822	790	769		796	772	754	773	790	742	734	739	760	784	771
Snout length	229	198			276	263	262	272	274	266	266	277	284	247	270
Orbit diameter	318	371	296	258	251	251	241	301	226	306	227	231	274	269	239
Interorbital width	191	240	300	327	286	281	290	303	277		294	292	304	337	314
Postorbital length	465	401	477		510	526	557	599	548	532	500	523	502	522	529
Orbit to angle preop.	389	401	419	424	469	491	508	510	500	500	484	492	491	467	500
Suborbital width	115	180	162	188	151	144	154	144	134	137	136	138	152	145	143
Length upper jaws	459	557	412	439	445	456	459	466	403	468	430	400	441	440	439
Preanal length	911							1,019	984				1,033	987	1,014
Outer pelvic to anal	306	407	204		104	123	134	129	94	116	125	138	122	131	129
Isthmus to anal	510		392	273	265	333	246	275	258			277	334	276	286
Greatest body depth	796		923	788		737		809	742	758		708	790	769	786
1D.–2D. Interspace	255		415	333	378	351	475	421		435	594	477		392	386
Height 1D.					510		508	502	484	532	625		502	493	414
Length 1P.				606	612	579	656	518	452	565			517	552	
Length 2P.				318		386		307	339	403		292		363	
Length outer gill-slit	248	293	208	179	184	175	187	178	156	165	164	172	175	183	176

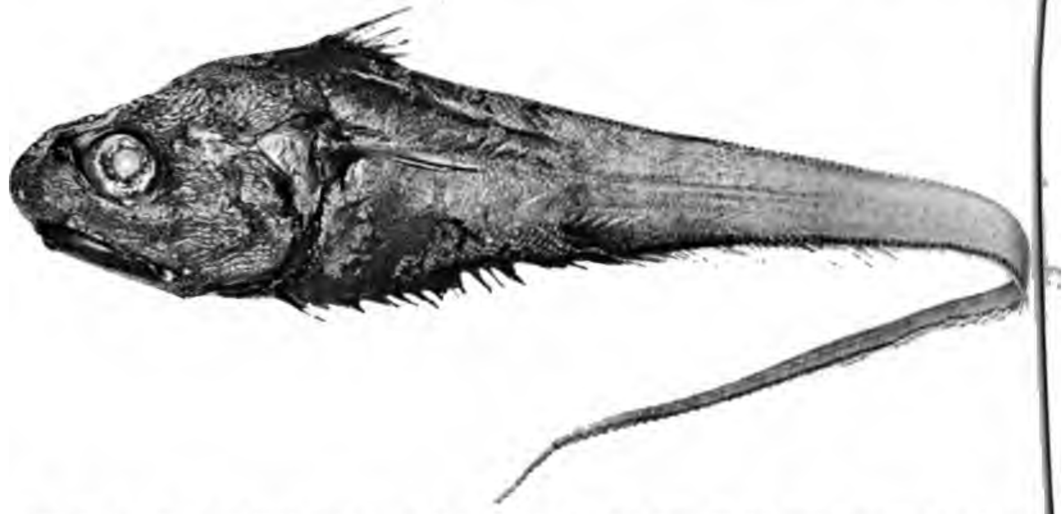


FIGURE 1. *Mesobius berryi* Hubbs and Iwamoto. Holotype, SIO 73–170, 61.8 mm HL, 344 mm TL, captured in midwaters the central equatorial Pacific at an estimated depth of 0–1280 m.

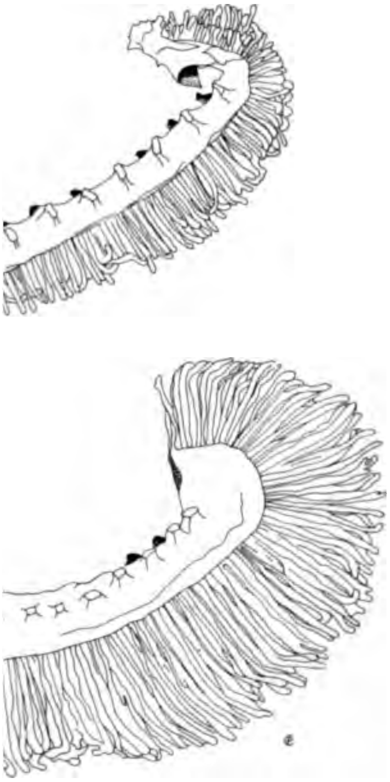
much farther forward than in most other macrourids (but about the same as in *Odontomacrurus murrayi* and *Cynomacrurus piriei* and in species of *Sphagemacrurus* and of subgenus *Lucigadus* of genus *Ventrifossa*). The posterior margin of the opercular bones are finely scalloped or crenulated. The interopercle is naked and scarcely exposed beyond the ventral and posterior margins of the large preopercle. The large lower jaw bears a pronounced knob at the symphysis. A small tubercle below the symphysis may be the remnant of a chin barbel. The gills occupy a relatively small portion of the capacious gill cavity; the tubercular rakers are widely spaced along the gill-arches. The short gill-filaments, measuring less than 1.5 in pupil diameter, are poorly developed in comparison with those of benthopelagic relatives (Fig. 2). The pyloric caeca are short and thick (some are bifid at the base); four central Pacific specimens yield 12, 13, 16, and 17 tips. Eleven abdominal vertebrae were counted in five specimens.

After examining four left-sagittal otoliths, John E. Fitch, California Department of Fish and Game, who provided the slide from which Figure 3 was taken, has stated (*in litt.*, 14 July 1975) that:

> "Very few kinds of fish show such a radical change in otolith shape as does *Mesobius*. Typically lobular margins are a juvenile character, except among cods and a few others in which they are a family character. The three smallest *Mesobius* otoliths show differences other than the juvenile lobular margins."

Fins: The first dorsal is small, with the greatest height less than the postorbital length. The first of the two spinous anteriormost rays is small and thornlike; its sharp leading edge is armed in some specimens with one or two minute denticles. The second ray is much longer, more slender, and near the base it is triangular in cross-section; its rather sharp leading edge bears small, often irregular serrations in most small specimens and in some large ones. The low second dorsal is poorly developed throughout. The relatively slender, pointed, narrow-based pectorals are inserted high on the body, much nearer the dorsal than the ventral body contour. The pelvics are small and slender. The anal is moderately well developed over its entire length and is much larger than the second dorsal. The pelvics originate below the posterior part of the preopercle; the anal origin lies below the pectoral base and below the anterior third of the first dorsal.

Scales: The scale structure is characterized in the diagnosis of the genus. The head is almost completely scaled except on the gill-membranes, lips, interopercle, and on the small narial fossa. In some specimens with heads longer than about 40 mm, the body scales, except those ventrally on the abdomen, over the nape, and around the base of the first dorsal, are devoid of spinules. The scales on the pectoral base are very thin, non-spinulated, and highly deciduous (only a few remain on one specimen). The orientation of



ht outer gill-arch of (A) *Mesobius berryi* and
'epis, comparing relative size of filaments of
Drawn by Cherryl Pape.

head scales (Fig. 4) and the as-
ule rows render the head surface
roups of varying, parallel courses.
nporal region the changing align-
nore or less sigmoidally curved
particularly conspicuous, from the
he orbit upward and backward over

er: The very small, elliptical blad-
all nib pointed posteriorly; in a 40-
imen the organ is 6 mm long. The
ca of the gas-bladder is thin and
but tough. What appear to be two
re enveloped in flocculent, white,
erial. Retia, attached to the gas
ge anteroventrally from the gas-

n: Partial dissection of a 64-mm-
(SIO 72–374) indicates that this
a relatively large oval or bean-
ture, presumably a light organ, en-

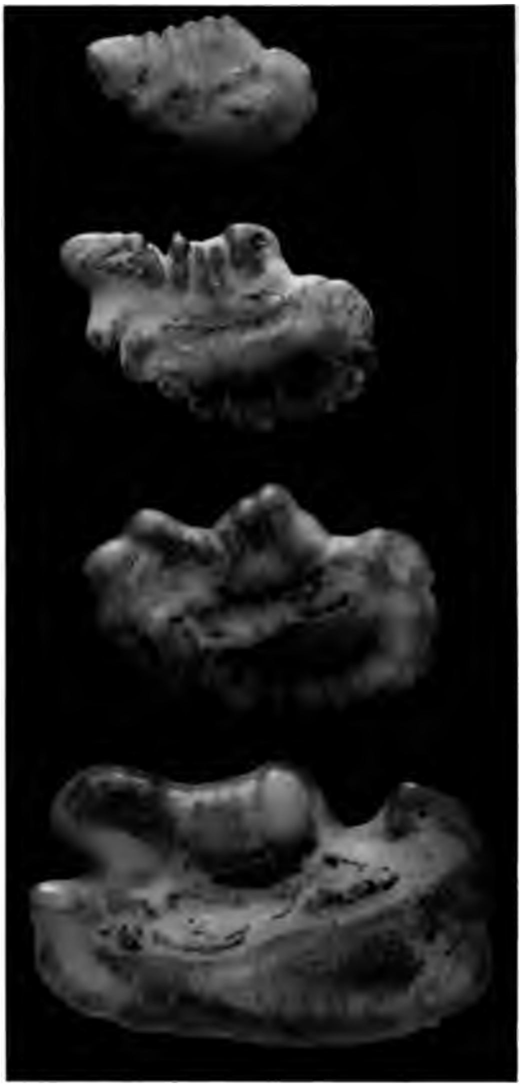


FIGURE 3. Otoliths (left sagittae) from four specimens of *Mesobius berryi*. Top to bottom: LACM 9585–20 (178 mm TL); LACM 30083–17 (26 mm HL, 190 mm TL); LACM 8638 (33 mm HL, 170 mm TL); LACM 9579–16 (70 mm HL, 392 mm TL). Otolith lengths are, respectively, 3.4 mm, 4.8 mm, 5.3 mm, and 7.1 mm. Photograph provided by John E. Fitch.

capsulated in a thin layer of muscle, and fronting the lower wall of the rectum. A midsaggital section through the organ (Fig. 5) reveals horizontally oriented folds of tissue with free borders posteriad. Anteroventral to the light organ is a small area, where the tissue is relatively translucent, that may serve as a "window" through which light is transmitted to the exterior. The absence of a large internal lens fronting the light

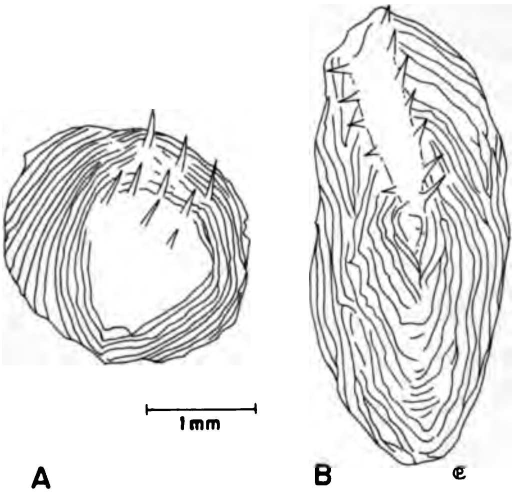


FIGURE 4. Scales from *Mesobius berryi*: (A) from below first dorsal fin; (B) from posttemporal region of head. Drawn by Cherryl Pape.

organ, so typical of most members of genera *Malacocephalus*, *Ventrifossa*, and *Nezumia*, indicates that *Mesobius* is a phylogenetically divergent member of the macrourid group characterized by having seven branchiostegal rays and an abdominal light organ.

Coloration in Alcohol: Adults are black or brownish black over the entire head and body, with a violet tinge over the trunk region. The tail surfaces are somewhat paler than the more anterior surfaces.

DESCRIPTION OF YOUNG.—A postlarva of 12 mm total length (SIO 72–14) has a head length of about 1.7 mm. The mouth is oriented almost vertically with the posterior end of the upper jaw lying on a vertical through the anterior edge of the eye. The diameter of the large eye measures less than 3 in HL, and is roundish, with a posterior bulge. The interorbital region is much narrower than the pupil. The abdomen is heavily pigmented with large melanophores. The anus is centrally located on the ventral midline. A black conical mass, the light organ, extends anteriad from the anus to between the bases of the pelvic fins. Rays of the anal fin appear to arise slightly anterior to the posterior end of the abdominal cavity. The pelvic-fin bases and the anus lie forward of the pectorals, which, in turn, lie slightly anterior to the origin of the first dorsal fin. The remarkably stylopterous pectorals are attached at the end of a slender pedicel about as long as the postorbital portion of the head.

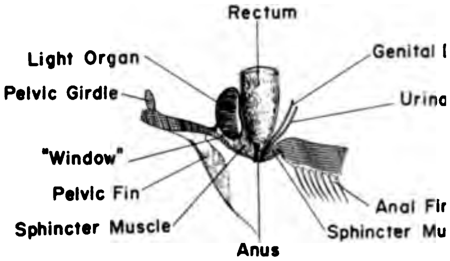


FIGURE 5. Diagrammatic illustration of midsaggital through rectum and light organ of *Mesobius berryi*.

Large prominent blotches occur on the
the tip of the lower jaws, the posterior a
each side of the lower jaw, the posterior
of the interorbital region, over the occip
gion of the skull, over the posttemporal
on the preopercle just behind the orbits,
the anterior edge of the base of the first
fin. A series of uniformly spaced saddle
extends along the dorsal margin of the ta
dashlike marks along the ventral margin
tail are spaced about half as far apart as
dorsal saddle marks.

An early prejuvenile (SIO 75–465; Fig.
mm in total length to tip of the broken t
essentially the same characteristics as t
the 12-mm specimen just described exce
the periproct region, the anal origin, and t
vic fins are situated somewhat farther fo
and the dashlike marks on the ventral pr
the tail are larger and more widely space
stylopterous pectorals are still well devel

In a 73-mm specimen (SIO 63–119), wit
about 6.3 mm long, the mouth is still
oblique. The interorbital space is slightl
rower than the pupil. The anus and pel
appear to have swung so far forward that t
directly under the hind end of the operc
base of the pectoral fin is no longer ped
but is reduced as in normal adults. De
along the leading edge of the second s
dorsal ray are slender, sharp, and well
oped. Spots on the head and body clos
semble those of a larger individual illustr
Figure 7 (top). The saddles below the
dorsal and the dash marks along the an
however, more numerous and more pro
especially posteriorly on the tail. Size-
changes in color pattern, from this si
closely parallel those described for *Odon*
rurus murrayi by Marshall (1964).

A prejuvenile specimen (Fig. 7, top) 1

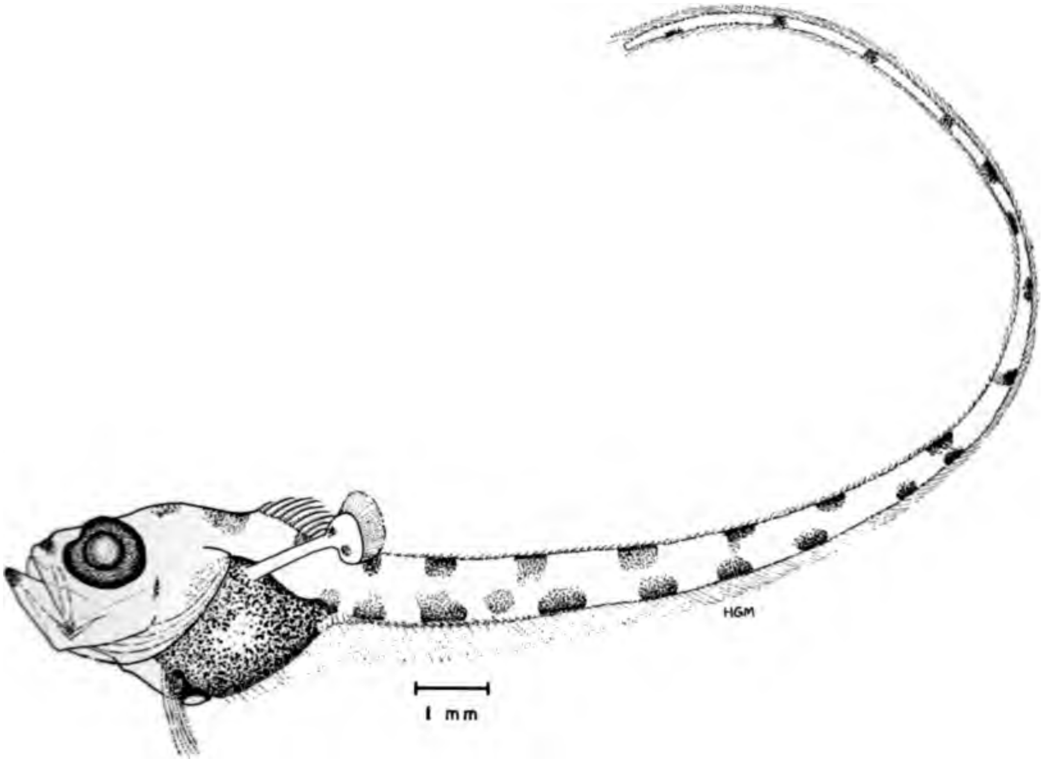


FIGURE 6. Early "phalacromacrurus" prejuvenile of *Mesobius berryi*, trawled in midwater at 31°15.0'N, 132°07.8'W, in the open eastern Pacific between southern California and Hawaii. Length 23.4 mm to broken tip of tail. Dorsal and anal rays diagrammatically shown. Drawn by H. Geoffrey Moser.

in head length (LACM 35671), does not differ significantly in general features from individuals half as large. The medium-brown trunk becomes paler posteriad on the tail to tan. The head is tan with scattered punctulations, and the body and head display series of large, prominent, circular, brown blotches as illustrated. A small dark spot is located dorsomedially on the nape, and there is another on the tip of the lower jaw. (In a specimen of comparable size (SIO H51–87, 16.7 mm HL), the spots are relatively smaller, and those along a file dorsally and midlaterally are more closely approximated.) The elongate scales on the head and the linear arrangement of the spinules on the scales are evident even at this early stage. Spinules are few on each scale, and they are slender, conical and erect. The circular scales on the body generally have only one to two spinules, and some scales along the ventral margins of the body and tail completely lack spinules.

In a somewhat larger individual (LACM 30083–17) of about 26 mm HL (Fig. 7, bottom), the overall color is much darker, generally brownish black. The blotches of the body are relatively smaller and are becoming obliterated by the dark ground color; a spot along the posterior base of the first dorsal fin, however, is very dark. In head and body configurations, this stage already resembles that of the adult. The mouth is nearly horizontal, the interorbital region is broad and rounded, and the ventral aspects of the trunk have already shifted posteriad approximately to their adult location.

A still larger individual (SIO 73–329), 40 mm in head length, has essentially the adult configuration and coloration—it is very blackish over the head and trunk, but slightly paler over the tail, on which faint traces of the lateral blotches still remain.

COMPARISONS.—A comparison of specimens from the eastern and from the central Pacific discloses no significant regional differences. Selected measurements and counts are tabulated

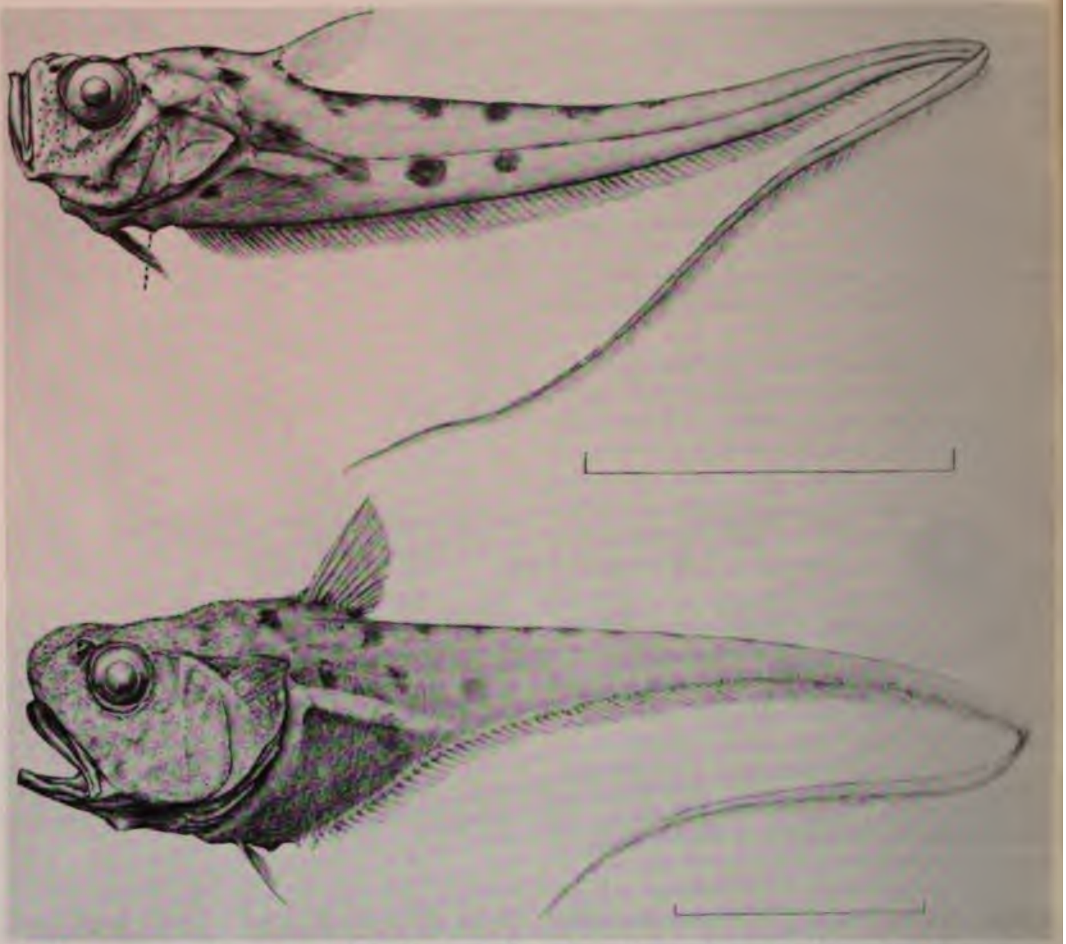


FIGURE 7. Diagrammatic illustrations of *Mesobius berryi* showing gross pigmentation patterns in juveniles 15.7 mm in head length (LACM 35671) (top) and 26 mm in head length (LACM 30083–17) (bottom). Fins and head partially reconstructed. Scales indicate 25 mm.

(Table 3) for the comparison of specimens from these two regions, and for contrast with the single New Zealand specimen of *Mesobius antipodum*. The flabbiness of the fish and the consequent difficulty in making accurate measurements calls for some reservation in evaluating the morphometric data.

The peculiar polka-dotted pigmentation pattern in early-life stages of *Mesobius* is not restricted to the genus but is also characteristic of the young of *Odontomacrurus*, *Malacocephalus*, and, possibly, *Sphagemacrurus*. Maul and Koefoed (1950) described two polka-dotted macrourids as representatives of a new genus and species, *Phalacromacrurus pantherinus*, but Marshall (1964) showed that their specimens were juveniles of *Odontomacrurus murrayi*. Marshall (1964:Fig. 3) also figured a polka-dotted juvenile of *Malacocephalus*. Backus et al. (1965) illustrated what they assumed to be a juvenile *Sphagemacrurus* (taken in the eastern Atlantic) that had a pigmentation pattern almost identical with that of *M. berryi*. We have attempted to borrow that specimen, which supposedly was deposited in the Museum of Comparative Zoology, but the curators there have reported their inability to find it. *Sphagemacrurus* is not, as far as we know, known from the eastern Pacific. Marshall (1973:514) considered *Macrurus trichiurus* Garman and *M. fragilis* Garman as belonging to that genus, but the junior author's examination of the holotypes has revealed that the former is clearly

:ific with *Nezumia convergens* (Garman)
latter is probably close to *Paracetonurus*
ll. The species of *Sphagemacrurus* have
›elvic fin rays as compared with 9 or
ı species of *Mesobius*.

genus *Odontomacrurus* is not known
ıe Pacific, as far as we know, although
ınoir (1969) reported two specimens of
·omacrurus pantherinus from the
hs of lancetfish, *Alepisaurus*, taken off
aledonia and New Hebrides. Mr. Four-
has informed us (*in litt.*, 16 Dec. 1975)
two specimens had apparently been dis-

cocephalus has not previously been
from the eastern Pacific, although repre-
'es are found in the Hawaiian Islands, off
in the Philippines, and in Australian wa-
'e have, however, examined one adult
:n of a *Malacocephalus* (Santa Barbara
History Museum no. 0061) taken off
ıarbara, California. It represents the only
›f the genus from the eastern Pacific. The
otted juveniles of *Malacocephalus* are
distinguishable from those of *Mesobius*
ing a chin barbel (developed even in a
:n (VIMS 03922) of *Malacocephalus* sp.
n HL), a pale esophageal portion of the
h (blackish in *Mesobius*), and a promi-
aleless area anterior to the periproct.

ɪɪʙᴜᴛɪᴏɴ.—*Mesobius berryi* has been
d in midwater nets fished as shallow as
ım to as deep as 0–2700 m. Most of the
s have been in trawls hauled to at least
›0 m, in waters off southern California,
a California (Mexico), off Oahu in the
ın Islands, and in the central North
8–10 degrees of latitude north of the
ın Islands, and in the equatorial mid-
off Christmas Island (Fig. 8). The species
ı to have a distribution pattern similar to
the myctophiform fish, *Evermannella*
ni, which is apparently "limited to areas
›nal in properties between major Pacific
water masses" (Johnson and Glodek
5). Unlike *E. ahlstromi*, however,
us berryi does not extend into the east-
t sector of the Pacific equatorial water
›ut is apparently replaced there by
a parini, the only other known
:lagic member of the family in the eastern
Ocean.

TABLE 3. *Mesobius* SPP. COUNTS AND MEASUREMENTS COMPARED BY LOCALITY. PROPORTIONAL MEASUREMENTS IN PERCENTAGE OF HEAD LENGTH. MORPHOMETRIC DATA FOR SPECIMENS SMALLER THAN 33 MM HL EXCLUDED.

Species	*berryi*		*anti-podum*
Location	Eastern Pacific	Central Pacific	New Zealand
No. of specimens	4	8	1
COUNTS:			
Gill-rakers on first arch	11–13*	10–13	15
Gill-rakers on second arch	10–12*	10–12	16
Pyloric caeca		12–17†	ca. 38
MEASUREMENTS:			
Total length (mm)	170–392	257–397	390
Head length (mm)	33–70	49–65	75
Snout length	24–27	26–28	32
Interorbital length	30–34	28–30	36
Preanal length	99–103	98–102	114
Outer pelvic ray to anal origin	12–13	9–14	19
Isthmus to anal origin	27–33	25–33	40
Body depth	77–79	74–81	84

* Counts from seven specimens.
† Counts from four specimens.

ɪᴏʟᴏɢʏ.—The species is named for Frederick H. Berry, now of the Southeast Fisheries Center, Miami Laboratory, of the National Marine Fisheries Service, who first collected the species, brought it to the attention of the senior author, and reported it as "Macrouridae, unidentified" (Berry and Perkins 1966:668).

MATERIAL EXAMINED.—*Holotype*. SIO 73–170 (61.8 mm HL, 344 mm TL): mid-equatorial Pacific, 00°03.8′–07.0′N, 154°56.0′W, midwater trawl; estimated fishing depth 0–1280 m, 3000 m.w.o.; R/V GEORGE MELVILLE cr. CATO 2, tow 82, 17 July 1973.

Paratypes. **Eastern Pacific** (8 specimens).—LACM 35671 (1, 15.7 mm HL, 165 mm TL): Mexico, off Isla Guadalupe, 29°30.0′N, 119°10′W; IKMT; 0–313 m, 3000 m.w.o., bottom depth 1850 m; R/V VELERO sta. 9904, 8 Aug. 1964.—LACM 8638 (1, about 33 HL, 170 TL); California, Santa Catalina Basin, 33°22′15″N, 118°45′00″W; midwater trawl; 1313–1298 m, 7000 m.w.o.; R/V VELERO sta. 10259, 13 Jan. 1965.—LACM 9579–16 (1, 70 HL, 392 TL): Mexico, off Isla Guadalupe, 30°30′20″N, 118°49′59″W; IKMT; about 1273 m.w.o.; R/V VELERO sta. 11226 30 Aug. 1966.—LACM 30083–17 (1, about 26 HL, 190 TL): Mexico, off Isla Guadalupe, 28°15′00″N, 118°12′00″W; 10-ft IKMT; about 919 m.w.o.; R/V VELERO sta. 12079, 14 April 1968.—SIO H51–87 (1, 16.7 HL, 182 TL):

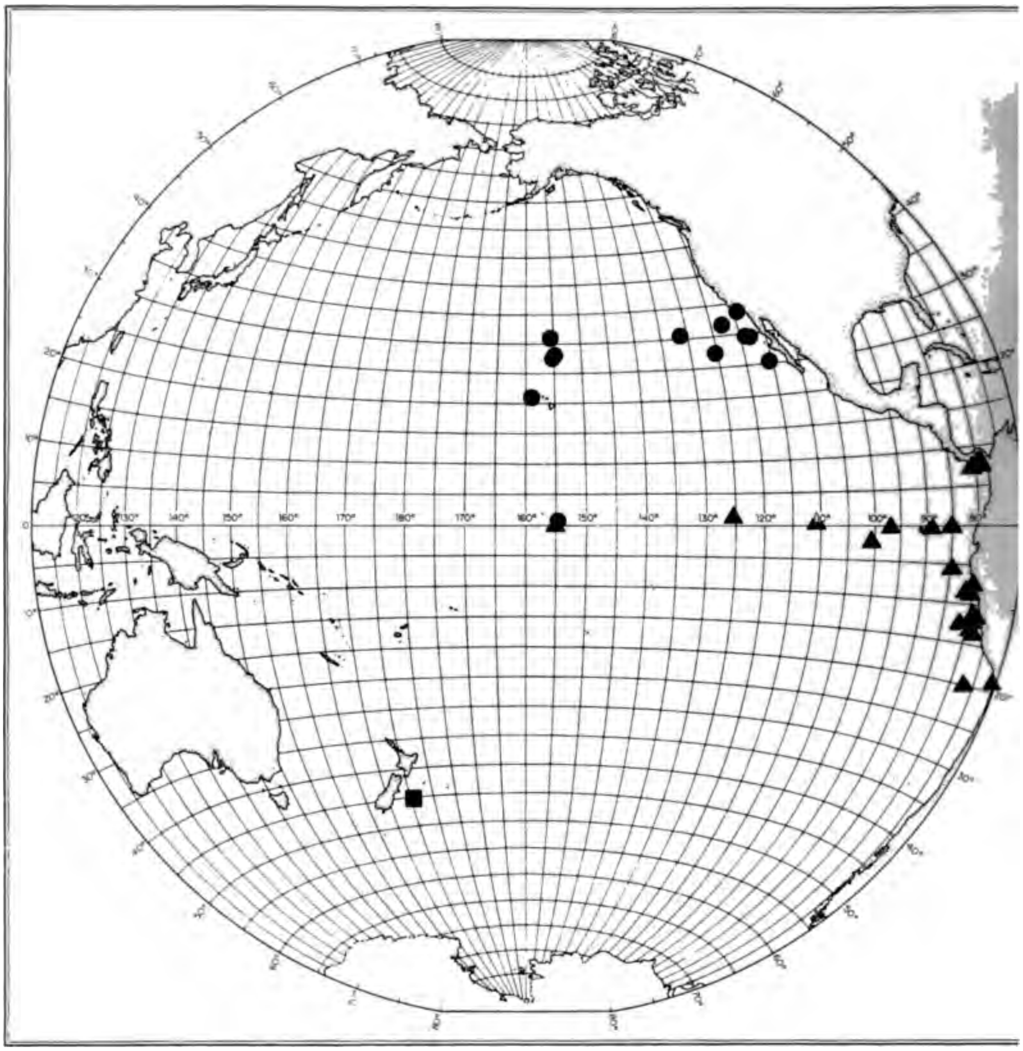
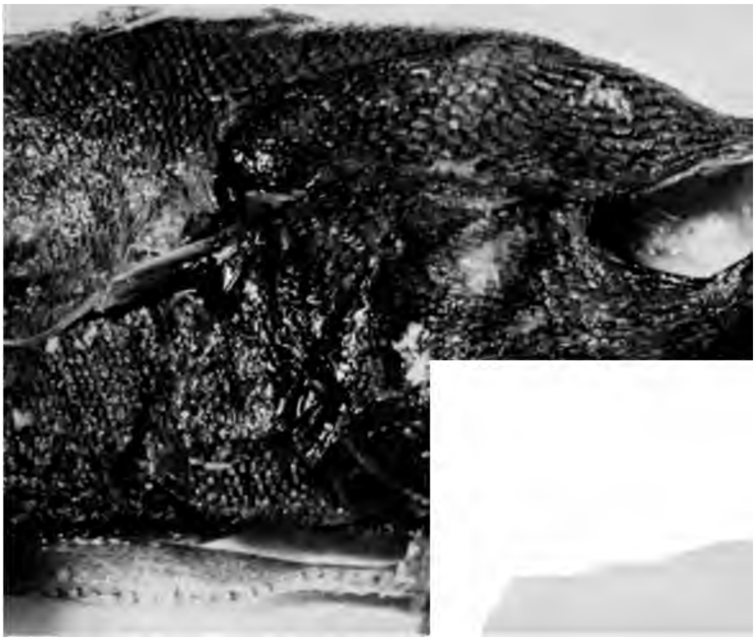


FIGURE 8. Distributions of *Mesobius berryi* (circles), *M. antipodum* (squares), and *Nezumia parini* (triangles).

Mexico, off Baja California Norte, 25°29′–31′N, 115°24′–09′W; midwater trawl; 1902 m, 21 Mar. 1951.—SIO 63–110 (1, about 6.3 HL, 73 TL): eastern Pacific W of Mexico, 27°22.6′N, 125°20.0′W; IKMT; 0–about 2700 m, 4500 m.w.o.; R/V HORIZON cr. 6204H, sta. 100.160, 16 Apr. 1962.—USNM 215327, formerly SIO 63–374 (2, 66–69 HL, 333–374 TL): California, WSW of San Diego, 32°07.3′–00.5′N, 122°39.5′–41.4′W; Cobb Pelagic Trawl Mark II; fishing depth about 640 m, bottom depth 4209 m, 1738 m.w.o.; R/V COBB cr. 58–7, sta. 86.92, 6 Mar. 1963.

Central Pacific (10 specimens).—CAS 20470 (1, 62 HL, 316 TL): SW of island of Oahu, Hawaii, 21°20′–30′N, 158°20′–30′W; 10-ft IKMT; fishing depth 1150 m, 3300 m.w.o.; R/V TERITU sta. 70–9–20, 21 Sept. 1970.—CAS 30469 (1, 49 HL, 257 TL): data as previous lot except depth about 1000 m, 2850–3000 m.w.o.; sta. 70–12–13, 11–12 Dec. 1970.—CAS 30471 (1, 61 HL, 340 TL): data as previous lot except depth 950–1000 m, 2700 m.w.o.; sta. 70–12–30, 16 Dec. 1970.—USNM 215326 (2, 57–62 HL, 307–345 TL): data as previou except depth 700–800 m, 2000 m.w.o.; sta. 73–9–24, 25 1973.—SIO 72–14 (1, about 1.7 HL, 120 TL): 27°20.6′–23. 155°20.7′–23.5′W, IK plankton trawl, 1000 m.w.o.; THOMAS WASHINGTON Exped. Aries 9, sta. PS1, 26 1971.—SIO 72–374 (1, 64 HL, 358 TL): 30°56.7′–59. 155°24.3′–16.3′W; Isaacs-Brown closing midwater trawl; ing depth 970 m, 1700 m.w.o.; R/V GEORGE MELVILL CATO 1, tow 41, 30 June 1972.—SIO 73–329 (1, about 40 221 TL): 28°03.5′–12.9′N, 154°38.8′–36.5′W; 10-ft 3000 m.w.o.; R/V THOMAS WASHINGTON cr. TASADAY I. 42, 22 June 1973.—SIO 73–327 (1, 65 HL, 397 TL): 27°5 28°07.2′N, 154°57.8′–155°07.5′W; 10-ft IKMT; 3000 m. R/V THOMAS WASHINGTON cr. TASADAY I, tow 17, 18 1973.—SIO 75–465 (1, 23.4 mm TL): 31°15. 132°07.8′W; oblique plankton tow hauled obliquely betw and 141 m, bottom depth 4691 m; R/V HORIZON cr. H620 sta. 70.200, 31 Mar. 1962.



9. Holotype of *Mesobius antipodum* Hubbs and Iwamoto. FAKU 47812, about 75 mm HL, 390 mm TL with tail e, from off South Island, New Zealand, in 995–1110 m.

us antipodum Hubbs and Iwamoto, new

8, 9, 10B; TABLE 3.)

NOSIS (based on one specimen).—A of the genus *Mesobius* with about 38 ranched pyloric caeca; medial gill-rakers arch 15, on second arch 16; snout length 32 percent of head length; interorbital bout 36 percent of head length.

NTS.—First dorsal fin II,9; pectoral fin lvic fin 7/7; gill-rakers in medial row on first arch and 2 + 1 + 13 on second cales below origin of first dorsal fin about scales below middle of first dorsal fin -9.

SUREMENTS.—Total length 390 mm (with mplete tail); head length about 75 mm. lowing proportional measurements are in dths of head length: postrostral length of 20; snout length 320; orbit diameter 227; bital width 360; postorbital length of head bit to angle of preopercle 467; suborbital 60; upper-jaw length 427; preanal length uter pelvic ray to anal origin 187; isthmus origin 400; greatest body depth 840; interspace between first and second dorsal fins 533; length pelvic fin 267; length outer gill-slit 172.

DESCRIPTION AND COMPARISONS.—Most features of this fish closely parallel those described for its congeneric relative *Mesobius berryi*. The high pyloric caeca count in this species results not from a larger caecal mass than found in *berryi* but rather from a greater branching of the mass to form more, and smaller, individual caeca. Larvae and juveniles are unknown, but we presume that individuals pass through a polka-dotted "phalacromacrurus" stage, as in *M. berryi*.

Because of the relatively poor condition of the holotype, and only specimen, precise measurements could not be made of most features. Differences between *M. antipodum* and *M. berryi* in morphometry (Table 3) may prove insignificant when additional specimens of *antipodum* are studied. Other features (meristic ones in particular), however, seem to confirm the differences suggested by the morphometric data. The holotype of *M. antipodum* appears to represent a much stouter, heavier-bodied species: the greatest breadth of the trunk is approximately

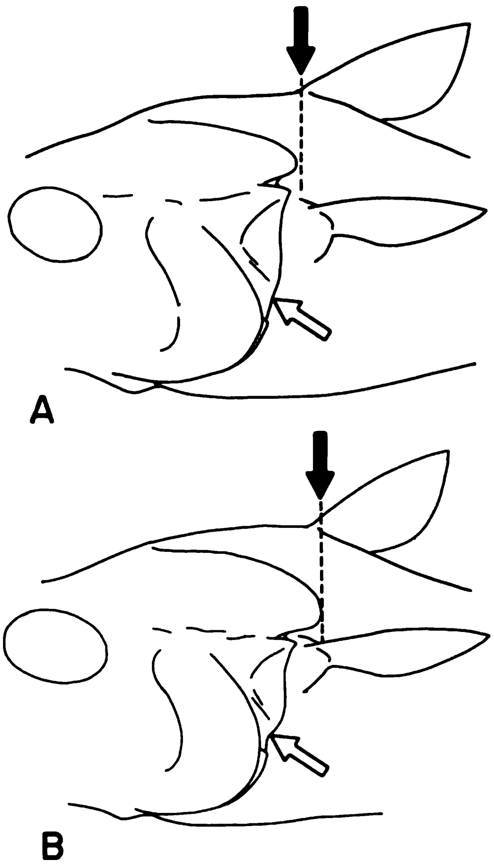


FIGURE 10. Diagram of posterior region of head of (A) *Mesobius berryi* and (B) *M. antipodum*, comparing the posterior extent of the posttemporal region (solid arrows) and the relative curvature of the subopercular margin (open arrows).

half the postrostral length of the head, whereas in *M. berryi* it is less than one-third that dimension. Although the holotype of *M. antipodum*, at 75 mm HL, is larger than the largest available specimen of *M. berryi*, the posterior nostril, at 2.8 mm, is much smaller (3.7 mm) than it is in the largest *M. berryi* specimen (LACM 9579–16, 70 mm HL). The shape of the opercle and suborpercle in the two species appears to differ (Fig. 10; *cf.* also Figs. 1 and 9). The posterodorsal arm of the opercle is relatively much longer in *berryi* than in *antipodum*, and the posterior margin of the subopercle is more strongly incurved in *antipodum*. Finally, the sharply marked posterior margin of the posttemporal region (Fig. 10) in this species lies above the base of the pectoral fin, whereas in *M. berryi* it scarcely extends beyond the posterior margin of the opercle.

Because only one specimen of *M. anti* is known, little can be said about the distri of the species. It would not be improba find that the species is widely distributed the southern hemisphere, especially in th ern sector, in temperate to tropical water

ETYMOLOGY.—The name is derived fr Latin *antipodum*, genitive of "antipodes ferring to persons dwelling at opposite poi the globe.

MATERIAL EXAMINED.—*Holotype*. FAKU 47812 (mm HL, 390 mm TL with tip of tail broken off): New Ze of South Island, 44°44'S, 175°42.0'E; 995–1110 m; KAI sta. 36, 16 July 1968.

Nezumia parini Hubbs and Iwamoto, species

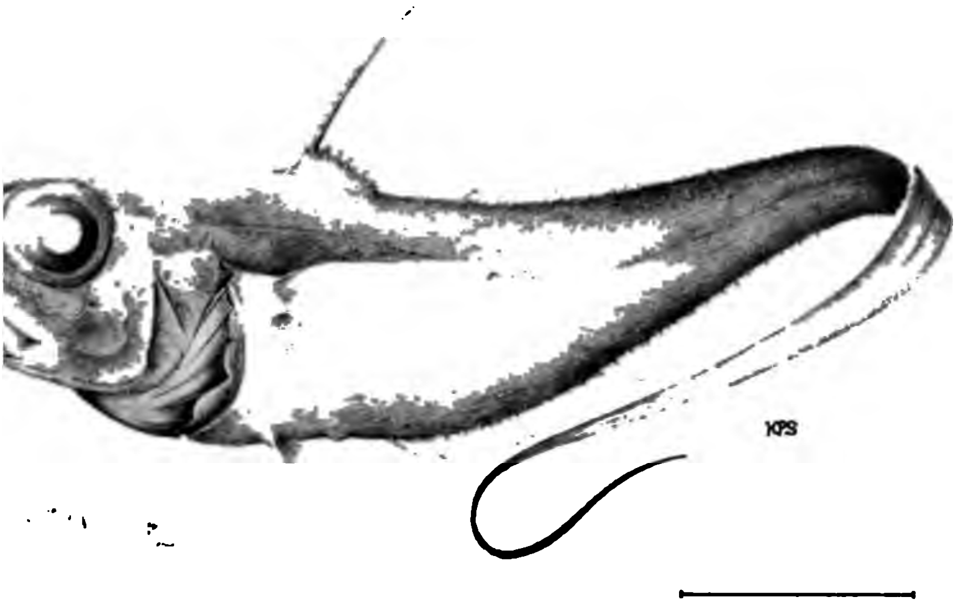
(FIGURES 8, 11; TABLES 4, 5.)

"A new bathypelagic species of *Nezumia*," Parin, Borodulina and Tchuvassov, 1973 (from English su p. 159).

Nezumia sp.: Parin, 1975: 321 (2 specimens fro Galápagos). Parin, Pokhilskaya, Sazonov and Fe 1976: 225 (description; 2 specimens).

DIAGNOSIS.—This distinctive bathy species of *Nezumia* is black. Each of the circular scales bears 1–15 long, slender, spinules that render the entire body surfa vety. Scale rows below the origin of the s dorsal fin number about 11–14, and the about 50 scales in the lateral line from its over a space equal to the predorsal lengt outermost of the short gill-filaments are l long as the pupil. The gill-rakers on the side of each of the first two gill-arches n 10–13 (usually 11–12). The outermost 11–12 pelvic rays is usually greatly prol 1.0 to 2.5 times as long as the head. Th bladder is rudimentary. The weakly dev lateral line is represented by a file of small lae.

DESCRIPTION.—*General Features:* C and measurements are given in Tables 4 The greatest width of the moderately co sed head is about two-thirds the greates depth. The bluntly pointed snout is armed spiny median scute and small, blunt, scutes. The interorbital region is gently c Except in young individuals, the orbit do quite enter the dorsal profile. The membranes are broadly attached to the is The outer gill-slit is restricted. The small, culear gill-rakers number 1–3 + 9–10



11. Holotype of *Nezumia parini* Hubbs and Iwamoto, SIO 73–165, 34 mm HL, 210 mm TL, from central equatorial nlarged dorsal and lateral views of scale from region between origin of second dorsal fin and lateral line (not drawn to ale indicates 25 mm. Drawn by Katherine P. Smith.

on the mesial side of the first arch, and 8–10 (total 10–12) on the second arch. The ments are much shorter than those in the losely related benthopelagic relatives and to be more fragile. The anus is located the middle third of the distance between lvic-fin base and the anal-fin origin. The r dermal window of the midventral light s externally evident as a small, teardrop- l fossa adjacent to the anus. The relatively thin, simple pyloric caeca branch near tachment to the wall of the pylorus; 21–29 were counted in four specimens. In a male pe (SIO 73–165) 30 mm in head length, the d rudimentary gas-bladder is only 2.5 mm ts drumming muscles are large (about 6 ng), but have no apparent direct connec- ith the gas-bladder; they originate an- on the body wall and are probably in- posteriorly to the mesentary around the dder. The lateral line is reduced to a of small, black papillae (free neuromasts?) that follow a course, from the posttemporal region posteriad onto the trunk and tail, similar to that of the lateral line in most macrourids. The sensory pores on the head are poorly developed.

Scales: The small, almost circular scales are armed with 1–15 (more in large specimens) long, slender, erect, terminally recurved spinules, arranged in 1–4 slightly divergent rows. Almost the entire head and body are uniformly scaled except on the ventral and anterodorsal surfaces of the snout, portions of the suborbital region, the gill-membranes, and the periproct. The base of the first dorsal, pelvic, and pectoral fins, and the mandibular rami, are sparsely and loosely scaled. The margins of the mandibles are often devoid of scales.

Fins: The fins are moderately well developed, although the rays are fragile. The outer pelvic ray is prolonged into a hairlike filament. The pelvic fins lie directly below the pectorals and anterior to the dorsal (these relative fin positions are somewhat exaggerated in the holotype (Fig.

TABLE 4. SELECTED MEASUREMENTS FROM 12 TYPE-SPECIMENS OF *Nezumia parini*. TOTAL LENGTHS AND HEAD LENGTHS IN MILLIMETERS; OTHER MEASUREMENTS IN THOUSANDTHS OF HEAD LENGTH. (HOLOTYPE INDICATED BY AN ASTERISK*.)

	ZMUC P372830	SIO 72–195	USNM 215324	ZMUC P372831	SIO H52–38	SIO 72–182	SIO H52–38	CAS 15996	SIO 72–195	SIO 72–195	SIO 73–165*	CAS 29414	Range
Total length	82	+75	104	91	118	+90	154	135	168	192	210	216	+75–216
Head length	14.8	15.4	16.8	17.7	19.0	21.0	21.9	24.4	30.2	31.9	34.0	35.0	14.8–35.0
Postrostral length	857	792	774	785	774	800	799	791	775	771	765	777	765–857
Snout length	271	260	250	249	226	276	233	246	252	251	241	234	226–276
Preoral length	271	201	244	215	216	233	274	246	228	226	264	234	201–274
Orbit diameter	364	377	381	367	374	380	406	369	361	345	368	395	361–406
Interorbital width	264	253	280	260	368	276	265	270	272	282	273	257	253–368
Postorbital length	463	403	417	373	352	371	397	410	361	382	411	375	352–436
Orbit to angle preop.	379	383	375	362	347	338	365	366	334	361	344	363	334–383
Suborbital width	143	130	119	153	147	124	135	123	119	129	134	114	114–153
Upper jaw length	357	338	327	316	321	329	310	320	331	313	318	315	310–357
Preanal length	1,286	1,883	1,280	1,158	1,263	1,309	1,461	1,137	1,325	1,285	1,559	1,371	1,127–1,883
Outer 2P. ray to A.	429	390	387	282	379	430	452	328	430	361	391	334	282–452
Isthmus to A. origin	643	584	625	508	658	667	776	574	695	627	647	620	508–776
Greatest body depth	786	714	792	650	806	762	806	779	861	878	853	886	650–886
1D–2D interspace	357		256	339	253	205	338	390	563	439	270	429	205–563
Height first dorsal				791	737		959			815	~588	886	588–959
Length pectoral fin	714	714	1,042	565		571			728	690	~588	600	565–1,042
Length pelvic fin			952			714	1,598		1,589	1,473	1,294	1,143	714–1,598
Length barbel	86	78	101	102	95	129	87	82	99	69	118	103	69–129
Length 1st gill-slit	214	195	185	170	168	186	146	164	136	146	153	172	136–214

5. Range, Mean ($\bar{X}$) and Standard Deviation Selected Counts Taken from Type-Specimens *ia parini* Hubbs and Iwamoto. Abbreviations: rsal Fin—1D.; Pectoral Fin—1P.; Pelvic Fin— -rakers on Medial Side of First Arch, In- Rudiments—GR I; Gill-rakers on Medial Side d Arch—GR II.

N	Range	$\bar{X}$	S.D.
20	9–11	10.30	0.80
36	13–19	16.03	1.30
39	10–12	11.00	0.32
20	10–13	11.40	0.68
20	10–14	11.55	0.89

les counts of both right and left fins from each , if possible.

to some dorsal flexure of the head in ation). The anal fin originates slightly vertical through the end of the first dor- . The first dorsal spine is small and e; the second is slightly prolonged and is long the leading edge with a file of small inelets.

tion: The small teeth form narrow bands jaw. Those on the premaxillary are nar- eparated at the symphysis, and those of r series are slightly enlarged.

ation in Alcohol: Some specimens are entirely black; others grade to dark h black. The buccal cavity is dark gray, gill cavity and the gill-filaments are pallid. The peritoneal membrane is a dark brown.

ibution.—*Nezumia parini* has been lly in open midwater nets fished at meso- ypelagic depths in the eastern and ial central Pacific (Fig. 8). The species is a narrow belt along the equator, from -Pacific to the coast of South America. ibution along the continental margin ap- stop at the Gulf of Panama in the north, thern Chile (at about 20°S) in the south. thern boundary of its range coincides southern extent of the oxygen-minimum Central America (Brandhorst 1959: Fig. ther this zone is limiting to the dispersal *rini*, as it is with many other midwater nay seem doubtful in view of the species' ice off Peru, where another oxygen- m layer is developed. Perhaps the thickness of the layer off Central a, where it may be more than 1200 m thick, forms an effective barrier to the northward dispersal of *N. parini*, while the less thick layer off Peru (maximum thickness about 800 m *fide* Wyrtki 1967) allows the species to reside below the oxygen depleted layer.

Relationships.—In its evolution *Nezumia parini* appears to have undergone considerable selection rendering it better adapted to a bathypelagic existence. These changes, however, have not obscured its basic relationship with that group of strictly benthopelagic species of *Nezumia* including *N. aequalis* (Günther) and *N. condylura* Jordan and Gilbert. Characters that indicate this relationship include: (1) the relatively sharply pointed, broad rostrum armed with a large spiny terminal and two lateral scutes; (2) the markedly angular and prominent suborbital ridge; (3) the relatively small and inferior mouth; (4) the restricted openings between the gill-arches; (5) the broadly connected gill-membranes; (6) and the relatively slender body. In varying degrees these characters contrast with those of the generally much larger species, that have in common a higher, blunter, narrower snout, a flatter suborbital region, a larger and more terminal mouth, wider openings between the gill-arches, less restricted gill-membranes, and a more laterally compressed and deeper body and head. Those contrasting species include *Nezumia atlantica* (Parr, 1946), *N. africana* (Iwamoto, 1970), *N. stelgidolepis* (Gilbert, 1891), *N. liolepis* (Gilbert, 1891), *N. holocentrus* (Gilbert and Cramer, 1897), *N. pudens* Gilbert and Thompson, 1916, and *N. bubonis* Iwamoto, 1974.

Evolutionary Remarks.—The discovery of a bathypelagic species of *Nezumia* is remarkable, considering that its closest relations are with species that are specialized toward feeding on benthic organisms rooted from the bottom. That *Nezumia parini*, in evolutionary terms, has not been long removed from a benthopelagic habit is reflected in its retention of features prevailing in its nearest relatives: in particular, a stout bony rostrum and suborbital ridge, a mental barbel, and a protrusible, inferior mouth. *N. parini* appears to have evolved the following features in adaptation to conditions in the bathypelagic realm: (1) entirely black or blackish color; (2) rudimentary gas-bladder; (3) short and thin gill-filaments; (4) vestigial lateral line; (5) small scales and thin, erect spinules that render the surface velvety; (6) much gelatinous intermuscular tissue; and (7) weak fin rays. Most of these features are shared in common with other strictly bathypelagic macrourids, as discussed by Marshall (1964). One can readily appreciate the advantages conferred by black color (camouflage), vestigial gas-bladder, reduced gill-filaments, gelatinous tissue, and weak fin rays (related to energy conservation and a slower life style). The peculiar scales are a puzzle, however—what advantages would they give? This scale type is developed in *Odontomacrurus*, *Cynomacrurus*, *Squalogadus*, *Macrouroides*, and, to varying degrees, in *Mesobius* and *Echinomacrurus*. In contrast to the small eyes found in these other genera (excepting *Mesobius*, which has moderate-size eyes), the eyes of *N. parini* are huge, measuring a third to two fifths of the head length. Perhaps the eyes are used more for detection of predator or prey than are the organs of the lateralis system (which seem to be less developed than those of its benthic relatives, especially along the trunk and tail). Feeding habits of *N. parini* are undoubtedly quite different from those of *Odontomacrurus murrayi* and *Cynomacrurus piriei*, if the large fanglike teeth, large terminal mouth and large, open head pores of the sensory lateralis system in the last two species are any indication. Feeding habits of the new species probably more closely approach those of *Squalogadus modificatus* and *Macrouroides inflaticeps*, both of which have small, protrusible, inferior mouths that are probably adapted to feed on small pelagic invertebrates and fishes. Juvenile macrourids taken at bathypelagic depths are often crammed with bathypelagic copepods. Perhaps *N. parini* feeds on similar organisms.

ETYMOLOGY.—We take deep pleasure in naming this highly distinctive species for our esteemed Soviet colleague Nikolay V. Parin, who has also recognized it as undescribed, and has very generously made his material available to us.

MATERIAL EXAMINED.—*Holotype*. SIO 73–165 (34 mm HL, 210 mm TL): mid-equatorial Pacific, 00°01.3'–0.2'S, 155°01.1'–154°59.8'W; IKMT; oblique tow, 1500 m.w.o.; R/V George Melville, cr. CATO 2, sta. 36, tow 71, 15 July 1972.

Paratypes. **Gulf of Panama:** ZMUC P372830 (1, 14.8 HL, 82 TL); 7°30'N, 79°19'W; stramin net with 150-cm opening; estimated fishing depth 0–1250 m, 2500 m.w.o., bottom depth 2550 m; Dana sta. 1203 XII, 11 Jan. 1922.—ZMUC P372831 (1, 17.7 HL, 90 TL); 6°48'N, 80°33'W; 300-cm ring-trawl; estimated fishing depth 0–1750 m, 3500 m.w.o.; Dana sta. 1208 IV, 16 Jan. 1922. **Galapagos:** PPSIO (1, 31 HL, + 164 TL);
00°17.5'S, 89°28.7'W; IKMT; 0–600–700 m; R/V A
Kurchatov sta. 313, sample N261, 10–11 No
Ecuador: PPSIO (1, 32 HL, 198 TL); 00°00.0'N, 8
IKMT; 1500–0 m; R/V Akademik Kurchatov st
sample N25, 28 Aug. 1968. **Peru:** PPSIO (1, 18 HL,
5°54.8'S, 84°53.8'W; IKMT; 0–1400 m; R/V Ak
Kurchatov sta. 227, sample N65, 5 Sept. 1968.-
215325 (1, 19 HL, + 108 TL); 7°43'–33'S, 80°43'
700–1110 m; R/V Anton Bruun cr. 18B, sta. 755
1966.—LACM 10279 (1, 18 HL, 90 TL); 7°47.5'S,
IKMT; 677 m; Eltanin sta. 34, 7 June 1962.—CAS
20.5 HL, 118 TL); 8°26'S, 80°26'W; IKMT; 2150–123
Anton Bruun cr. 16, sta. 650H, 9 June 1966.—CAS
17–24 HL, 111–135 TL); 11°50'–52'S, 78°16'–24'
0–1350 m, bottom depth 1640 m; R/V Anton Bruu
sta. 656P, 16 June 1966.—SIO 65–603 (1, 33 HL,
11°51'–12°06'S, 79°04'–78°58.5'W; 10-ft IKMT; ca. 0
5630 m.w.o.; R/V Anton Bruun cr. 12, sta. 1,
1965.—CAS 29414 (1, 35 HL, 216 TL); 11°52'–53'S
19'W; IKMT; 0–900 m; R/V Anton Bruun cr. 16, s
13 June 1966.—USNM 215324 (1, 16.8 HL, 104 TL)
55'S, 79°06'–78°53'W; IKMT; 0–455 m, bottom depth
R/V Anton Bruun cr. 16, sta. 656A, 12 June 1966.-
(2, 26–37 HL, 140–221 TL); 12°20.0'S, 81°42.5'
0–1500 m; R/V Akademik Kurchatov sta. 229, sam
7–8 Sept. 1968.—PPSIO (1, 23 HL, + 125 TL); 1
78°31.9'W; IKMT; 0–1500 m; R/V Akademik Kurch
277, sample N198, 25 Oct. 1968.—SIO 72–195 (4, 1
75–192 TL); 13°51.3'S, 77°41.1'W; 10–ft IKMT; estim
ing depth 0–1100 m, 3000 m.w.o.; R/V Washingto
Tow Exped., sta. MV72–II–38, 12–13 May 1972. C
72–182 (1, 21 HL, 90 TL); 18°38.4'–35.1'S, 70°39.0'-
10–ft IKMT; estimated fishing depth 0–940 m, 2500
R/V Washington SouthTow Exped., sta. MV72–I
May 1972.—PPSIO (1, 35 HL, 230 TL); 20°00.0'S, 76
IKMT; 0–1500 m; R/V Akademik Kurchatov sta. 2
ple N112, 17 Sept. 1968. **Equatorial Pacific:** PPSIO (1
+ 104 TL); 00°01.4'S, 97°02.7'W; IKMT; 0–700
Akademik Kurchatov sta. 1454, sample N98,
1974.—PPSIO (1, 14 HL, + 70 TL); 00°01.4'S, 97
IKMT; 0–410–420 m; R/V Akademik Kurchatov s
sample N112, 19 Jan. 1974.—SIO 69–496 (1, 29 HL,
02°20'–12'S, 100°42.5'–27'W; 10-ft IKMT; 0–675
m.w.o., bottom depth 3292 m; R/V Washington st
16–MWT, 26 Nov. 1969.—SIO H52–38 (2, 19–22 HL,
TL); 00°17.7'N, 110°26'W; 7 June 1952.—PPSI
HL, 245 TL); 01°59'N, 125°19'W; IKMT; 0–900–100
Lira trawl 51, 27 Mar. 1966.—SIO 73–171 (1, 36 HL,
00°07.0'–06.6'S, 154°56.0'–155°01.4'W; IKMT; obliq
3000 m.w.o.; R/V Melville cr. CATO 2, sta. 36, to
July 1972.—SIO 73–165 (1, about 30 HL, 185 TL); d
as for holotype.

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.I, No. 8, pp. 253–265; 1 fig., 1 table. **October 20, 1977**

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CURRENT SERIAL SERVICE

RDS OF THE GENUS *LEPIDODACTYLUS* (GEKKONIDAE) FROM E INDO-AUSTRALIAN ARCHIPELAGO AND THE ISLANDS OF THE PACIFIC, WITH DESCRIPTIONS OF NEW SPECIES

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ABSTRACT: An annotated list and a key to species of the genus *Lepidodactylus* recorded from the Indo-Australian Archipelago are presented; four new species (*L. magnus, L. mutahi, L. novaeguinea,* and *L. orientales*) from New Guinea and the Solomon Islands are described. The relationships and distribution of the species are discussed.

INTRODUCTION

e revising Philippine species of the genus *dactylus*, one of us (Brown) examined s, including types of extra-Philippine . In the course of these comparisons, it : evident that the Indo-Australian species *idodactylus*, with the exception of the *s-woodfordi* complex, comprise two distinct from the species in the Philip- Also recent extensive collections from iuinea and the Solomons include previ- mdescribed species. It seems most ap- te to present these results in a report e from our monograph, currently in prep- , on the gekkonid lizards of the Philip-

ACKNOWLEDGMENTS

We are deeply indebted to Drs. A. G. C. Grandison of the British Museum (BMNH), Jean Guibé of the Muséum National d'Histoire Naturelle, Paris (MNHN), K. Klemmer of the Senckenberg Museum (SM), W. R. Heyer of the United States National Museum of Natural History (USNM), E. E. Williams of the Museum of Comparative Zoology (MCZ). H. Marx of the Field Museum of Natural History (FMNH), R. G. Zweifel of the American Museum of Natural History (AMNH), C. J. McCoy of the Carnegie Museum (CM), Paul Webber of the Australian Museum (AM), J. Menzies of the University of Papua New Guinea (UPNG), and N. Kwapena and M. C. Downes of the Department of Agriculture, Stock, and Fisheries, Papua New Guinea as curators for the Papua New Guinea Museum (DASF or PNGM), for the privilege of

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rch Associate, Department of Herpetology, California Academy of Sciences.

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TABLE 1. Counts, measurements and pertinent ratios for species of *Lepidodactylus*.

									Ratios		
Species (No. of Specimens used)	Snout-Vent Length at Maturity	No. of Pores (♂)	No. of 4th Toe Scansors	No. of 1st Toe Scansors	No. of Divided Scansors on 4th Toe	Terminal Scansor Entire or Divided	Webbing Between 3rd & 4th Toes	No. of Upper Labials	Eye Diameter / Snout Length	Head Breadth / Snout-Vent Length	Hind Limb Length / Axilla-Groin Distance
Group I											
L. listeri (4)	40.8–46 (2♂)	11–14	11–13	8–10	0	entire	base+	10–12	74–84%	20–22%	83–89%
L. magnus (20)	50–71 (15♂)	38–49	10–13	10–12	0	entire	1/8±	10–12	80–88%	17–20%	74–84%
L. manni (7)	38.6–42.7 (2♂)	12–13	9–12	8–10	0	entire	base+	9–12	79–88%	20–22%	72–87%
L. mutahi (15)	37.2–56 (16♂)	27–34	10–11	8–10	0	entire	1/4±	11–12	79–90%	17–20%	73–84%
L. oorti (3)	53.7–57 (2♂)	28–29	13–14	9–10	0	entire	base+	10–12	67–72%	20–21%	73–80%
L. orientalis	37± (1♂)	19 (1)	10–11	8–9	0	entire	base–1/8	10–11	69–86%	18–19%	67–78%
L. pumilus (18)	38.4–45.0 (4♂)	31–40*	11–12	8–9	0	entire	1/3–1/2	10–12	81–94%	14–16%	59–67%
Group II											
L. gardeneri (1)	45.3 (1♂)	—	12	11	2–3	entire	base+	11	75±%	17±%	71±%
L. guppyi (20)	37.5–48.2 (10♂)	39–51	11–13	8–10	2–4	entire	1/4±	11–13	78–88%	16–19%	67–77%
L. novaeguineae (15)	36.7–41.2 (7♂)	11–18	11–16	8–11	1–3	entire	1/4–1/3	9–12	85–97%	16–20%	65–77%
L. pulcher (3)	54± (1♂)	16	17–19	10–13	2–3	entire	1/4–1/3	10–12	70–85%	18–19%	81–85%
L. shebae (1)	36.2 (1♂)	32	11		2	entire	1/8	10	78±%	16–17%	—
Group III											
L. lugubris	37.3–48	19–26	11–15	9–11	3–4	divided	1/8±–1/4	10–12	75–85%	17–22%	74–87%

amining pertinent material. CAS and CAS-SU
er to collections at the California Academy of
iences. I am also deeply indebted to my col-
igues Dr. Alan E. Leviton and Mr. Robert C.
ewes for their assistance and suggestions. Il-
strations were prepared by L. Meszoly of the
useum of Comparative Zoology, Harvard
niversity, and W. Zawojski of Stanford Uni-
rsity. This study is part of the Philippines-
cific Islands research project under the aus-
ces of National Science Foundation Grant
B-41947.

SYSTEMATIC SECTION

The available keys to *Lepidodactylus*, such as
ose of Taylor (1922) and de Rooij (1915) have
t proven satisfactory to the non-specialists.
r this reason, we have combined a more or
ss typical key to species-groups with diagnoses
species which should prove more useful.

IAGNOSTIC KEY TO SPECIES OF *LEPIDODACTYLUS* OCCURRING IN THE INDO-AUSTRALIAN RCHIPELAGO AND ISLANDS OF THE PACIFIC

(See Table 1 for additional data on species.)

a. A relatively small species, adults usually less than 50 mm snout-vent length; terminal and 2–4 subterminal scansors on all digits but first divided (Fig. 1a); range of fourth toe scansors 11–15, covering distal 3/4 to 4/5 of toe; tail usually moderately flattened, with lateral fringe evident (rarely subcylindrical); usually parthenogenetic; males, when present in populations, with about 20–30 preanal and femoral pores .... *L. woodfordi-lugubris* complex

b. Terminal scansor on all digits entire or slightly notched (Fig. 1b); subterminal scansors entire or a few distal ones divided; tail subcylindrical without lateral fringe 2

a. One or more (usually 2–4) subterminal scansors divided medially (Figs. 1b and 1d) 3

b. All scansors entire, or at most, with only shallow median notches (Figs. 1c and 1e) 6

a. Enlarged scales of pore-series and pores limited to preanal region or including only 1 or 2 scales on proximal part of thigh; no greatly enlarged scales on rest of thigh; usually 20 or fewer preanal pores in males 4

3b. Enlarged scales of pore-series not limited to preanal region, at least one or more rows of scales on thigh distinctly enlarged although they may be separated from preanal series; 25 or more preanal and femoral pores in males 5

4a. An intermediate-sized species, adults about 40–55 m snout-vent length; 16–19 fourth toe scansors, covering toe to base (Fig. 1d); 11–13 first toe scansors; ¼ to ⅓ webbed between third and fourth toes; 18–20 enlarged scales in preanal pore-series, bearing 16 pores for one male; brown blotches on head and nape (sharply outlined for Wild Island specimens), length of hind limb more than 80% of axilla-groin distance .... *L. pulcher*

4b. A small species, adults about 36–45 mm snout-vent length; 11–16 fourth toe scansors, covering approximately distal ¾ of toe; 8–11 first toe scansors; 1/6 to 1/4 webbed between third and fourth toes; 16 to 20 enlarged scales in preanal pore-series, bearing 12–19 pores for males; length of hind limb about 65 to 75% of axilla-groin distance; blotches on head and nape not sharply outlined .... *L. novaeguineae* new species

5a. A relatively small species, 45± snout-vent length (one available adult); 12 fourth toe scansors, covering distal ¾ of toe; 11 first toe scansors; webbed only at base between third and fourth toes; the unique holotype, female, with about 38–39 enlarged preanal and femoral scales in position of pore-series, covering basal ¾ plus of thigh .... *L. gardeneri*

5b. A small to moderate-sized species, adults usually less than 50 mm in snout-vent length; 11–13 fourth toe scansors, covering distal ⅔ to ¾ of toe (Fig. 1b); 8–10 first toe scansors; about ¼ to ⅓ webbed between third and fourth toes; 40–52 enlarged preanal and femoral scales in position of pore-series, continuous and extending almost to distal end of thigh; bearing 39–52 pores (sample of 9 males) .... *L. guppyi*

5c. A relatively small species, about 36 mm snout-vent length for known adult specimen; digits moderately dilated; 11± fourth toe scansors, 2 subterminal ones divided; toes 1/5 to 1/4 webbed; unique holotype (a male) with about 34 enlarged preanal and femoral scales in the position of the pore-series, continuous, bearing 32 pores .... *L. shebae*

6a. Adult size relatively small; enlarged scales of pore-series and pores limited to the preanal region or with only 2 or 3 on proximal part of thigh; usually 20 or fewer preanal pores in males; webbed at base to 1/6 between 3rd and 4th toes 7

6b. Adult size variable; 26–50 or more enlarged preanal and femoral pore scales in the position of the pore-series, in either a continuous series or separate preanal and femoral series; 25 or more preanal and femoral pores in a continuous or separate series in males 9

7a. Small to moderate-sized species, adults usually less than 50 mm snout-vent length; digits relatively broadly dilated; 9–12 undivided fourth toe scansors, covering distal ¾ of toe; 8–10 first toe scansors; webbed at base or to 1/6 between third and fourth toes; usually 18 or fewer scales in position of pore-series, limited to preanal region or with only one or two such scales on base of thigh; bearing 15 or fewer preanal pores in males; (see note under Discussion) .. 8

7b. A relatively small species, 37 to 43 mm snout-vent length (3 adults); digits long and relatively slender; 10–12 undivided fourth toe scansors, covering approximately distal ⅔ of toe; 20–24 enlarged scales in pore-series, confined to the preanal region or only a few on base of thigh; bearing 19 preanal pores (sample of one male) .... *L. orientalis* new species

8a. Limited to Fiji Islands in central Pacific Ocean .... *L. manni*

8b. Limited to Christmas Island in Indian Ocean .... *L. listeri*

9a. Usually ¼ or more webbed between third and fourth toes; usually 12 or fewer scansors beneath the fourth toe.......... 10

9b. Usually only 1/5 or less webbed between third and fourth toes; usually more than 12 scansors beneath the fourth toe...... 11

10a. A relatively small species, 34 to 48 mm snout-vent length (12 adults); digits relatively short and broadly dilated; 11–13 entire fourth toe scansors, covering the distal ½ to ⅔ of the toe (Fig. 1e); ⅓ to ½ webbed between third and fourth toes; 12–15 enlarged scales in preanal pore-series, separated by several scales (7 to 12 in samples) from moderately enlarged femoral series; bearing 11–14 preanal pores separated from femoral series of 10 to 14 in males; length of hind limb about 59 to 70% of axilla-groin distance .... *L. pumilu*

10b. A moderately large species, adults from about 40 to 55 mm snout-vent length; digits moderately dilated; 10 or 11 entire fourth toe scansors, covering approximately the distal ⅔ of toe; about ¼ webbed between third and fourth toes; 28–36 enlarged preanal and femoral pore scales, extending almost to distal end of thigh; bearing a continuous series of 27–34 pores in males; length of hind limb usually more than 70% of axilla-groin distance .... *L. mutahi* new specie

11a. A relatively large species, 53 to 57 mm snout-vent length (3 adults); digits moderately dilated; 12–14 entire fourth toe scansors; 9 or 10 first toe scansors; webbed at base only between third and fourth toes; 32–36 enlarged preanal and femoral pore scales in continuous series, extending over proximal ⅔ of thigh; bearing 28–30 pores in males...... *L. oor*

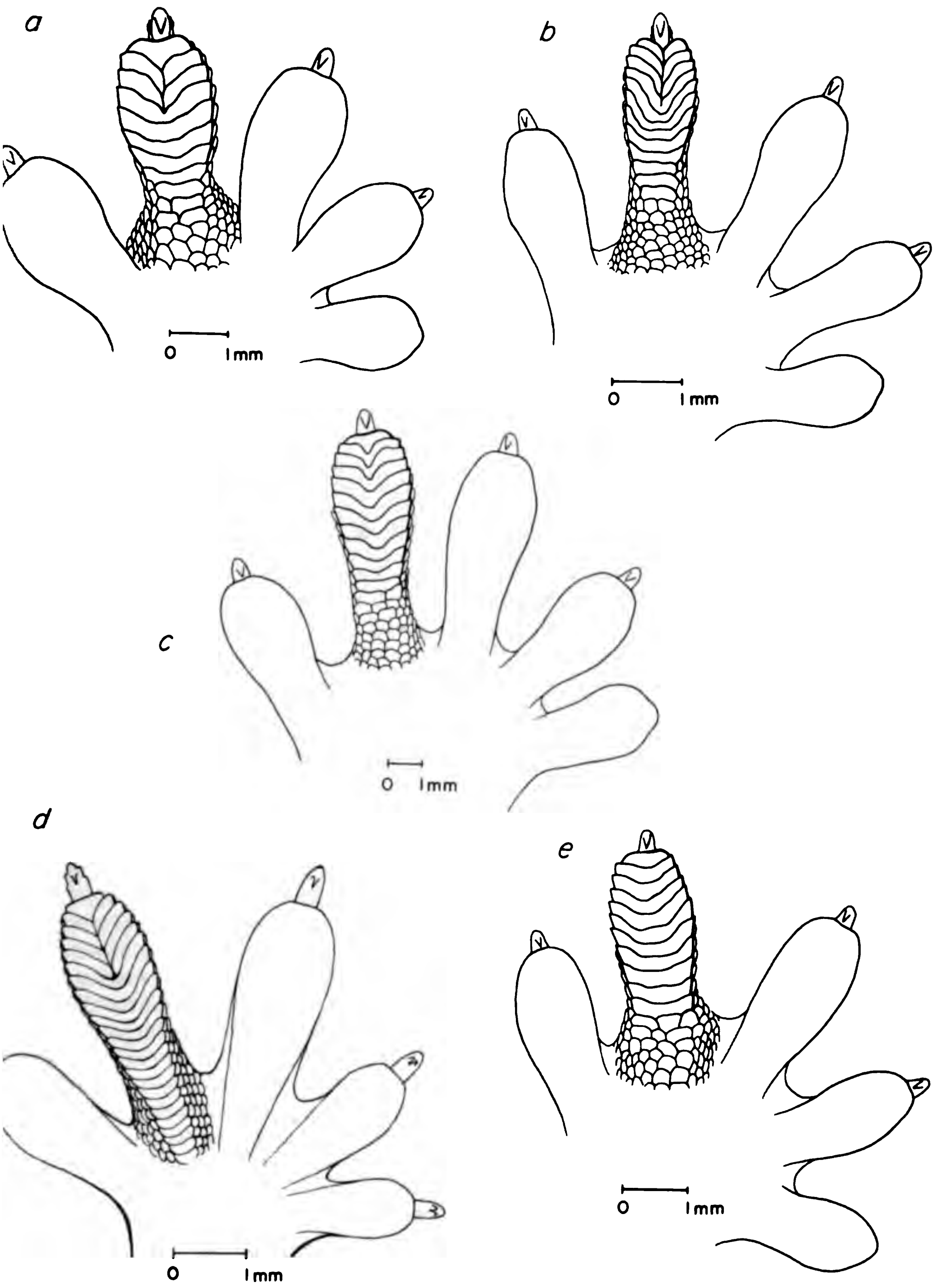
11b. A large species, adult males measure 50 to 71 mm snout-vent length; 12–15 entire fourth toe scansors (Fig. 1c); 10–12 first toe scansors, 1/6 to 1/5 webbed between third and fourth toes; 40–50 enlarged preanal and femoral pore scales in a continuous series, extending almost to distal end of thigh; bearing 38 to 49 pores in males .... *L. magnus* new speci

Lepidodactylus Species of the Indo-Australian Archipelago and Islands of the Pacific

Lepidodactylus gardeneri Boulenger

Lepidodactylus gardeneri Boulenger, 1897:306 (ty locality: Rotuma Island, Polynesia; type in BMNH).

Material Examined.—BMNH 1946.8.22.35 (holotype



IGURE 1. Inferior view of foot of five species of *Lepidodactylus*: (a) *L. lugubris*; (b) *L. guppyi*; (c) *L. magnus*; (d) *L. pulcher*; *L. pumilus*.

RANGE.—The known range is the type-locality, Rotuma Island.

Lepidodactylus guppyi Boulenger

Lepidodactylus guppyi BOULENGER, 1884:210 (type-locality: Faro Island, Solomon Islands; holotype in BMNH).

MATERIAL EXAMINED.—BMNH 84.3.2.54 (holotype); 1972.223–4, 1973.218; CAS 139650; MCZ 65862, 67122, 67124, 67126, 74517–19, 75904 ab, 75905, 115559, and 115563–65.

RANGE.—This species has been recorded from Bougainville, Buka, Faro, Guadalcanar, Kolambangara, Malaita, Puruata, Savo, Sterling, and Tulagi Islands in the Solomons. Hediger (1934:490) also lists *L. guppyi* as occurring in New Britain.

Lepidodactylus listeri (Boulenger)

Gecko listeri BOULENGER, 1888:535 (type-locality: Christmas Island, Indian Ocean; syntypes in BMNH).

Lepidodactylus listeri KLUGE, 1967:9

MATERIAL EXAMINED.—BMNH 1946.8.25.91 (holotype), 1905.6.24.16–17, 1909.3.4.7; MCZ 143838; CAS 16861.

RANGE.—This species is known only from Christmas Island in the Indian Ocean.

Lepidodactylus lugubris (Duméril and Bibron)

Platydactylus lugubris DUMÉRIL AND BIBRON, 1836:304 (type-locality: Otaiti (= Tahiti) Island, Polynesia; holotype in MNHN).

Peropus neglectus GIRARD, 1858:197 (syn. *fide* M. A. Smith 1935; type-locality: Rio de Janeiro, Brazil; holotype lost).

Hemidactylus meijeri BLEEKER, 1859:47 (syn. *fide* M. A. Smith 1935; type-locality: Bintang, Rhio-Archipel *fide* M. A. Smith; holotype in BMNH).

Gecko moestus PETERS, 1867:13 (syn. *fide* M. A. Smith 1935; type-locality: Palau Islands; holotype in Berlin Museum).

Gymnodactylus caudeloti BAVAY, 1869:13 (syn. *fide* M. A. Smith 1935; type-locality: New Caledonia; repository data not available).

Peripia mysorensis MEYER, 1874:129 (syn. *fide* M. A. Smith 1935; type-locality: Mysore (= Biak Island); holotype in Berlin Museum).

Peripia ornata MCLEAY, 1878:98 (syn. *fide* Kluge 1963; type-locality: Port Moresby, New Guinea; type lost).

Lepidodactylus divergens TAYLOR, 1918:242 (syn. *fide* M. A. Smith 1935; type-locality:Great Govenen Island, Sulu Islands, Philippines; type lost).

MATERIAL EXAMINED.—MNHN 5323a-b (syntypes); AMNH 65484–87, 66223, 69628, 41867, 41875–77, 41880–87; CAS 50274–96, 60613–18, 62485–86, 72031; CAS-SU 9159–60, 9173, 9175–76, 9178, 9189, 12164–66, 12176–81, 18047–56, one hundred plus uncatalogued; DASF 10297–99, 11462, 11853–60; FMNH 44504, 73377 (paratype, *L. divergens*); MCZ 16403, 19646, 27936, 33518, 48625–31, 49496–97, 69499, 69501a-b, 26087–88 (paratypes, *L. divergens*), 85747–50, 26091–93, 135431–32, 137648–50, 140981; USNM 28239, 68044–46, 68048, 68866, 70736, 119195, 121387, 121398.

RANGE.—This species has a wide distril
in the tropics, extending from India, Sri
(Ceylon) and nearby islands through sou
Asia, Philippines, Indo-Australian Archip
northern Australia, islands of the tr
Pacific, and western Mexico and C
America.

Lepidodactylus magnus, new species

Holotype: MCZ 101504, an adult male, collected b
ginbotham in the Kol Jim Valley Highlands, Pap
Guinea, 28 Mar. 1967.

Paratypes: Central mountain area of New Guinea
about longitude 142° and 146° E, Lufa area: MCZ 9
Karimui area: MCZ 101505–07, 101509; Nondiri are
91602–06, AMNH 98513–14; Yandime area: MCZ 91
AMNH 98512; Orumba area: MCZ 91589; Yangamu
MCZ 91597; Chauve area: MCZ 91598–99; Elmaga
MCZ 91601, CAS 139656; Huon Peninsula: MCZ 542
diawa area: 109242; Irumbafoie area: MCZ 91591–96,
1974.4217, AMNH 95209–13; Kaironk Valley: UPN
17, CAS 139654–55, FMNH 197933, CM 59037, MNH
USNM 198147; Gono: AMNH 92527–43 + 18 uncat
CAS 139830; Kassam: AMNH 92653; Lalang: AMN
Rugli: AMNH 105880–92; Kwi Valley: MCZ 91597.

DIAGNOSIS.—A large *Lepidodactylus*,
vent length about 50 to 70 mm for adults;
long, moderately dilated, *Gekko*-like; dist
thirds or more of ventral surface bearing
vided scansors, though one to four subte
ones may occasionally exhibit shallow no
12 to 13 scansors beneath fourth toe; 10
beneath first toe; toes webbed at base be
first and second toes and about one-four
tween third and fourth toes; adult male
about 40 to 50 preanal and femoral
femoral series extending from base to ne
distal end of thigh; sometimes disrupted
femoral series or between preanal and fe
series by one or a few scales; tail subcylin
without lateral flange or spines.

DESCRIPTION.—A large *Lepidodac*
snout-vent length 50 to 70+ mm in 12
males (one 43-mm male immature), 55 to
in 10 mature females, and 24.5 to 25.9 mm
25 to 27 mm before preservation) in four
lings; moderately depressed, neither st
robust nor slender in appearance; snout s
tapered, rounded, length 38 to 41+% of
of head; internasal distance 46 to 49% of
length; head breadth 72 to 80% of head
and 17 to 20% of snout-vent length; diam
eye about 80 to 88% of snout length;
about 1-½ times as broad as long, som
longer between supranasals than at latera

ostril surrounded by rostral, first upper
supranasal and two enlarged scales
posteriorly; supranasals separated by two
e scales (most frequently three) bordering
; 9 to 12 upper labials, eighth to tenth be-
nedian plane of eye; 9 to 10 lower labials,
r ones as large as triangular mental; first
scales behind mental gives appearance of
ort chin shields followed by two to three
f slightly enlarged scales; scales on snout
than those on dorsal and lateral surfaces
y, which are covered by small, relatively
n granular scales, enlarged tubercles lack-
nbs moderately developed, length of ex-
hind limb (in preserved condition) 75 to
f axilla-groin distance; toes webbed at
etween first and second and as much as ¼
en third and fourth; digits moderately di-
throughout their length (*Gekko*-like);
h of fourth toe about 35 to 42% of its
to base of web; 10 to 13 (most frequently
tire scansors under fourth toe, covering
imately distal ⅔ to ¾ of toe (Fig. 1c); 10
cansors under first toe; all digits but first
and toe clawed; compressed, clawed
ges free only at end of dilated part, ex-
g short distance beyond; a series of about
arged scales in position of preanal and
al pore-series, bearing 40 to 51 pores in
e males, preanal series forming a broad,
ed arch and femoral series extending al-
o distal end of thigh; (femoral series often
ts some breaks of one to three or four
without pores); pore-series followed by
l rows of enlarged scales in preanal region
ly by a single row on thighs before meet-
naller, more granular scales of posterior
e; tail appears subcylindrical, depth just
ior to basal swollen area 74 to 90% of its
th at same point, and tail breadth 53 to 62%
d breadth; lateral margin without flange of
r spines; scales on ventral surface of tail
than on dorsal surface, squarish or at
fused to form quadrangular platelike
(see also Table 1).

or. *In preservative*: dorsum and upper lat-
rfaces grayish tan or brown, varying from
ely uniform or with a few dark lines or
es along dorsolateral area to a pattern of
r six diffuse, wide, irregularly margined,
erse bands between nape and base of tail;
rather uniformly light to heavily flecked
rown. *In life*: neck, body, and tail varying
from pale grayish brown through dark gray-brown to brown; neck and body pattern often with shallow W-shaped bars; tail with pale blotches having distinct anterior border, fading posteriorly into darker ground color to next pale blotch; a pale stripe from ear to axilla and usually from posterior corner of eye to ear; often a pair of dark stripes dorsolaterally on neck and usually a very distinct dark vertebral stripe on base of tail, reaching only to first or second pale blotch; frequently with pale spots around ear, and some specimens with pale spots on dorsum and in a line midlateral surface.

Measurements (in mm) of holotype: snout-vent length 70.7; axilla-groin distance about 34.5; hind limb length 27; length of head 16.7; breadth of head 13.8; snout length 6.7; diameter of eye 5.7; internasal distance 3.2; interorbital distance 3.3; tail breadth at base 7.3; tail depth at base 6.1.

ECOLOGICAL NOTES.—The localities listed for the holotype and paratypes are in the central mountains at elevations between about 1000 and 2000 meters. One of us (Parker) and Professor J. I. Menzies have observed the species in crevices of limestone cliffs, among dead leaves, particularly of *Pandanus* and banana trees, and occasionally in houses, especially those built of bush material. These are resting sites during the day. The species is active at night. Pairs of eggs were found in a vertical fissure in a limestone cliff at Irumbafoie. Two large eggs were also present in the oviducts of several gravid females.

Lepidodactylus manni Schmidt

Lepidodactylus manni SCHMIDT, 1923:51 (type-locality: Suene, Viti Levu, Fiji Islands; holotype in MCZ).

MATERIAL EXAMINED.—MCZ 16880 (holotype), AMNH 81746–51.

RANGE.—This species is known only from the Fiji Islands.

Lepidodactylus mutahi, new species

Holotype: MCZ 127844, an adult male, collected by Fred Parker in Mutahi area, Bougainville Island, Solomon Islands, 17 May 1966.

Paratypes: Bougainville Island, same locality as holotype: MCZ 118317–118321; Tinputz area: MCZ 118316; Kieta area: MCZ 64152, 69216; Kunua area: MCZ 75863–75866, 75869, 77590–77593, BMNH 1974.4218, UPNG 5192; Torokina area: USNM 120875–76, 120880, 120882, CAS 139657.

DIAGNOSIS.—An intermediate-sized *Lepidodactylus*, snout-vent length 37 to 56 mm for adults; digits moderately dilated (*Gekko*-like); scansors covering approximately distal ⅔ of ventral surface of fourth toe; scansors undivided but often two to four subterminal ones with shallow notches; toes webbed about ¹/₅ between the first and second and about ¼+ between third and fourth; adult males with 29 to 34 preanal and femoral pores in a continuous series, extending almost to distal end of thigh; tail subcylindrical without lateral fringe of skin or spines.

DESCRIPTION.—An intermediate-sized *Lepidodactylus*, snout-vent length 37 to 56 mm for 16 mature males, 43 to 50 mm for five mature females; habitus moderately depressed, moderately slender; snout tapered, tip broadly rounded, its length about 39 to 42% of head length; internasal distance 40 to 50% of snout length; breadth of head 67 to 75% of head length and 17 to 20% of snout-vent length; diameter of eye 79 to 90% of snout length; rostral much broader than long and usually with a mid-dorsal bulge between the supranasals; nostril surrounded by rostral, first upper labial, supranasal, and two enlarged scales dorso-posteriorly; supranasals usually separated by two or three scales (rarely one) which border rostral; 10 to 12 upper labials, usually ninth or tenth beneath center of the eye; 9 to 11 lower labials, anterior ones larger than triangular mental; latter followed by four, occasionally five, rows of enlarged scales in position of chin shields, anterior rows largest; scales on snout larger than those on dorsal and lateral surfaces of body which are covered by small, relatively uniform, granular scales; enlarged tubercles lacking; limbs moderately developed, length of extended hind limb (in preserved condition) 73 to 87% of axilla-groin distance; toes webbed, about ¹/₅ between first and second, usually about ¼ between third and fourth; digits moderately dilated, long; greatest breadth of fourth toe about 37 to 41% of its length to base of web; 9 to 12 undivided scansors beneath fourth toe, covering about distal ⅔ of toe; 11 to 14 under third toe and 8 to 10 under first toe (Table 1); all digits but first finger and toe clawed; compressed, clawed phalanges rising free at end of dilated part and extending for only short distance beyond; a series of 30 to 36 enlarged scales in position of pore-series; preanal series chevron-shaped, femoral series extending almost to distal end of thigh; a continuous series of 27 to 34 preanal and femoral pores in males; preanal series followed by several rows of enlarged scales and preceded by two or three of slightly enlarged scales; femoral series i ing an isolated enlarged row; tail subcylind depth just posterior to basal swollen area 92% of breadth at same point, and breadth 51% of head breadth (one example greater 50%); lateral margins of tail without flan skin or spines; scales on ventral surface c somewhat larger than those on dorsal su and somewhat squarish.

Measurements (in mm) of holotype: s vent length 55.2; axilla-groin distance length of hind limb 19.8; head length 14.9; breadth 9.8; snout length 5.6; diameter of 4.2; tail breadth 5.0; tail depth 3.6; intern distance 2.2.

Color. *In preservative*: dorsal ground varies from gray-tan to brown, often with r vague darker blemishes; venter uniformly or with brown flecks which are most num laterally. *In life*: dorsum varies from yellow-brown to dark red-brown; often w light stripe from eye to ear; usually o patches on the tail; black blotches or bars v are evident on dorsum of many individual pear in life to vary for any given individua are assumed to change in response to stimulus.

ECOLOGICAL NOTE.—Field observation the Kunua area (by Parker) indicate the sp is most abundant in *Pandanus* in perm coastal swamps, but that it also occurs in b trees and newly cleared garden areas.

RANGE.—Known at present only from gainville Island.

Lepidodactylus novaeguineae, new species

Lepidodactylus pulcher (part). LOVERIDGE, 1948:334; WERMUTH, 1965.

Holotype: CAS 89684, collected in Lake Sentani area Irian, by E. S. Herald, 1944.

Paratypes: West Irian: BMNH 1938.6.6.72, FMNH 60; Hollandia area, West Irian: AMNH 66346; Fin area, Marobe District, Papua New Guinea; CAS-SU 29, 12182, USNM 118824–25, 159826–27; Guisika area. Peninsula, Papua New Guinea: USNM 119428, AMNH 66667, MCZ 49612; Mt. Nibo, Sepik District, Papu Guinea: AMNH 100209–10.

DIAGNOSIS.—A moderate-sized *Lepidod lus* distinguished by the following combinati characters: about 36 to 41 mm snout-vent l for 7 mature males; 11 to 14 scansors be the fourth toe, covering approximately the

e toes; 8 to 11 beneath first toe (16 to 19 and
13, respectively, for *L. pulcher* with which
s has been confused); tail subcylindrical
t fringe or spines; terminal scansor on all
entire; a few subterminal ones, one to
on fourth toe divided; enlarged scales in
eries limited to preanal region, about 14 to
l bearing 12 to 18 pores in males; toes
¼ to ⅓ webbed.

CRIPTION.—A relatively small *Lepidodac-*
snout-vent length about 36 to 44 mm in
; habitus not strongly depressed; snout
y tapered and broadly rounded, its length
35 to 39% of head length; internasal dis-
48 to 58% of snout length; breadth of head
81% of head length, and 16.5 to 21% of
vent length; diameter of eye 85 to 97% of
length; rostral about twice as broad as
quadrangular to slightly trapezoidal; nos-
rounded by rostral, first labial, supranasal
o enlarged scales dorso-posteriorly; sup-
ls usually separated by two scales which
the rostral; 9 to 12 upper labials, eighth or
eneath the center of the eye; 9 to 12 lower
, the anterior ones larger than the triangu-
ntal; four or five rows of somewhat en-
scales, in same position as chin shields,
or row or two most enlarged; scales on
larger than those on dorsal and lateral sur-
of body, which are covered by relatively
m granular scales; enlarged tubercles lack-
mbs moderately developed, length of ex-
d hind limb (in preserved condition) 66 to
f axilla-groin distance; digits about 1/6 to 1/3
ed, about 1/6 between first and second toes,
to ⅓ between third and fourth toes; digits
broadly dilated, noticeably more so in dis-
lf; breadth of fourth toe 37 to 40% of its
to the base of the web; terminal scansor
l digits entire; two or three subterminal
ors divided medially; 11 to 16 scansors be-
fourth toe, covering about the distal ⅔;
gits but first finger and toe clawed, com-
ed, clawed phalanges rising free at end of di-
part and extending for only a short distance
d; about 16 to 20 enlarged scales in posi-
f pore-series, bearing 11 to 19 pores in ma-
nales (sample of three), limited to preanal
n or with one or two at base of thigh; tail
lindrical, depth just posterior to basal
en area about 75 to 85% of breadth at a
sponding point, and tail breadth about 47 to
of head breadth; lateral margin without
fringes or spines; scales on ventral surface of tail larger than those on dorsal surface and more or less squarish in shape (see also Table 1).

Color. *In preservative*: dorsal ground color rusty-tan to grayish, often with vague brownish markings; in some a little lighter in middorsal region and usually rather vague, reddish-brown flecks and markings on dorsal and dorso-lateral surfaces; or occasionally a *woodfordi*-like pattern of diffuse light and dark transverse bands; tail dorsally with a pattern of diffuse to fairly sharp, irregular, tan and reddish-brown cross bands.

Measurements (in mm) of holotype: snout-vent length 40.1; axilla-groin distance 20.1; length of hind limb 15.4; head length 10.1; head breadth 8.1; snout length 3.9; diameter of eye 3.3; tail breadth 4.5; tail depth 3.8; internasal distance 1.9.

ECOLOGICAL NOTE.—Loveridge (1948:334) notes that one of the Gusiko specimens was collected on the trunk of a coconut palm and the other beneath the bark of a dead tree.

RANGE.—Known from Hollandia area, West Irian to Huon Peninsula in northern Papua New Guinea.

Lepidodactylus oorti (Kopstein)

Gekko oorti KOPSTEIN, 1926:77 (type-locality: Teun and Seruna Islands, Banda Sea and Samlakki, Tanimbar Islands; syntypes in BMNH, Leiden Museum and MCZ).
Lepidodactylus oorti KLUGE, 1967:9.

MATERIAL EXAMINED.—BMNH 1946.8.25.9, MCZ 38970 and 39721 (3 syntypes).

RANGE.—The species is known only from the Banda and Tanimbar Islands in the East Indies.

Lepidodactylus orientalis, new species

Gekko pumilus BOULENGER, 1898:697 (not Boulenger, 1885a:473).

Holotype: BMNH, 1897–12–10–7, collected in the Port Moresby area, Central District, Papua New Guinea, by Dr. L. Loria.

Paratypes: Port Moresby area, Central District, Papua New Guinea: PNGM 10025, Konedobu, Central District, Papua New Guinea: MCZ 147357 and CAS 139833.

The holotype of this previously undescribed species was one of three referred by Boulenger (1898) to *G. pumilus*. We have not seen the other two of Dr. Loria's specimens, but we assume they are still in the museum at Genoa.

DIAGNOSIS.—A relatively small *Lepidodactylus* distinguished by the following combination of characters: snout-vent length 37 to 43 mm for four adults; digits moderately dilated (*Gekko*-like); 10 to 11 scansors covering ½ to nearly ⅔ of ventral surface of fourth toe; scansors undivided, but two or three subterminal ones often with shallow notches; about $^{1}/_{6}$ webbed between third and fourth toes; adult males with a series of 19 plus or minus preanal pores; enlarged scales in pore-series not extending beyond one or two scales on the base of the thigh; tail subcylindrical without lateral fringe of skin or spines.

DESCRIPTION.—A relatively small *Lepidodactylus*, snout-vent length 37 to 43 mm in four adults; habitus moderately depressed, rather slender; snout tapered, tip broadly rounded, its length about 41 to 43% of head length; internasal distance about 50% of snout length; breadth of head 72 to 76% of head length and 18 to 19% snout-vent length; diameter of eye 69 to 86% of snout length; rostral broader than long, usually with a median, dorsal groove; nostril surrounded by rostral, first upper labial, supranasal, and two enlarged scales dorso-posteriorly; supranasals usually separated by two scales which border the rostral; 10 to 11 upper labials, usually the eighth or ninth beneath the center of eye; 9 or 10 lower labials, anterior ones larger than mental; latter followed by three or four rows of enlarged scales in position of chin shields; scales on snout larger than those on the dorsal and lateral surfaces of the body, which are covered by small, relatively uniform, granular scales; no enlarged tubercles; limbs moderately developed, length of extended hind limb (in preserved condition) 67 to 78% of axilla-groin distance; toes weakly webbed, at base to about $^{1}/_{6}$ between third and fourth toes; digits moderately dilated, long; greatest breadth of fourth toe about 40% of its length to the base of the web; 10 to 11 undivided scansors beneath the fourth toe; usually two or three subterminal ones slightly notched; scansors covering distal $^{3}/_{5}$ to $^{2}/_{3}$ of fourth toe; 8 or 9 undivided scansors beneath the first toe (Table 1); all digits but the first finger and toe clawed, the compressed, clawed phalanges rising free at the end of the dilated part, but extending only a short distance beyond; a series of about 20 to 24 enlarged scales in position of pore-series including only one or two scales on basal end of thigh, and bearing, for males (one example), 19 preanal scales in a continuous series; the series followed by several rows of enlarged scales between it and vent; tail subcylindrical, depth just posterior to basal swellings 74 to 82% of breadth at s
point, tail breadth 56 to 67% of head brea
lateral margins of tail without flange of ski
spines; scales on ventral surface of tail la
than those on dorsal surface.

Color. *In preservative*: dorsal ground
grayish tan to tan, with two or three pair
small- to moderate-sized, brown, dorsolat
spots in region of fore limbs; dorsum, tail
limbs marked by faint to relatively promin
narrow, irregularly margined, brownish, tr
verse bands, separated by somewhat bro
light areas.

Measurements (in mm) of holotype: sn
vent length 37.1; axilla-groin distance 1
length of hind limb 13.0; head length 9.1;
breadth 6.8; snout length 4.0; diameter of
3.2; tail breadth 3.8; tail depth 3.1; intern
distance 2.1.

ECOLOGICAL NOTE.—We have no hat
data for this species.

RANGE.—Known only from Konedubo
Port Moresby, Central District, Papua
Guinea.

Lepidodactylus pulcher (Boulenger)

Lepidodactylus pulcher BOULENGER, 1885b:166 (type-loc
Wild Island, Admiralty Islands; syntypes BMNH).

MATERIAL EXAMINED.—BMNH 1946.9.8.48–50 (synt
PNGM 10294, 10296, CAS 139832.

RANGE.—This species is known from Wil
land off the northwest coast of Manua Isl
Admiralty Islands, and Plot and Lengendr
islands on the southeast coast.

Lepidodactylus pumilus (Boulenger)

Gecko pumilus BOULENGER, 1885a:473 (type-locality:
ray Island, Torres Straits; type in BMNH).
Lepidodactylus pumilus, KLUGE, 1967:9.

MATERIAL EXAMINED.—BMNH 1946.8.25.93 (holo
MCZ 135353–55, 135364–66, 135529–30, 137568, 13
139420, 141048–49, 141366–68, AM 44233, PNGM 10293,
139834.

RANGE.—This species is recorded from
ray and Hammond islands, Torres Straits,
Daru Island of southeast New Guinea, Wes
District, Papua New Guinea.

Lepidodactylus shebae (Brown and Tanner)

Pseudogekko shebae BROWN AND TANNER, 1949:43
locality: Lower Lunga River, Guadalcanar Island, Sol
Islands; type in the Museum, Brigham Young Univer
Lepidodactylus shebae, KLUGE, 1967:9.

rerial Examined.—Brigham Young University 7002 ype).

.NGE.—This species is known from Guadal- r, Solomon Islands.

lodactylus woodfordi Boulenger

dactylus woodfordi Boulenger, 1887:334 (type- ity: Faro Island, Solomon Islands; type in BMNH). : Discussion.)

rerial Examined.—BMNH 1946.8.22.34.

.NGE.—This questionable species has been ded from the Solomon Islands, New ea, Philippines, and islands of the Pacific ı.

lodactylus species

ry small samples (1 to 3 specimens) from ollowing populations have not been referred y of the designated species because of some rences in characters studied. We have not ned these to a species pending the availabil- f larger samples.

unique specimen from Mount Riu on idest Island, Louisiade Archipelago, .MNH 76766, female) is close to *L. orien- lis* in most characters but the interdigital ebbing is more extensive.

wo examples from the Adelbert Mountains Madang District, Papua New Guinea, .MNH 105087–88, male and female) appear ost closely related to *L. magnus* based on e webbing and the shape of their digits but e most like *L. pumilus* in size and, possibly, the pore pattern of males.

wo specimens, BMNH 1974.3027 from 'aigue Island and an uncatalogued example om Jappen Island, both off the northwest ew Guinea coast, are close to *L. waeguineae* in most characters but appear rger.

hree specimens, MCZ 135433–34, 139418, ature males, from Ndrova Island, Admiralty lands, are close to *L. guppyi* but are smaller 1.5 to about 38 mm snout-vent length) and ive slightly fewer pores (34–36).

Discussion

luge (1967) pointed out some of the larities and differences among the related tonid genera *Gekko, Pseudogekko, dodactylus,* and *Hemiphyllodactylus*. By numerical weighting (as a method of quantifying a judgment as to the degree of advancement exhibited for eleven characters analyzed), he ranked *Pseudogekko, Lepidodactylus,* and *Hemiphyllodactylus* in that order of change from an assumed *Gekko*-like ancestor. Kluge's approach enabled him better to define the genera and, in so doing, it became necessary to reassign several species within these genera, including some from *Gekko* to *Lepidodactylus* (Kluge 1967:332).

Russell (1972) included *Gekko, Pseudogekko, Luperosaurus, Ptychozoon, Lepidodactylus, Hemiphyllodactylus, Gehyra,* and *Perochirus* in a related group, the *Gekko*-group of the subfamily Gekkoninae. Within the genus *Lepidodactylus,* he regarded the evidence from the foot structure as supporting the hypothesis of an evolutionary trend involving a distal shift and reduction in number of subdigital scansors, accompanied by a median division of some of the distal ones to form two rows. We believe the evidence also indicates that a more depressed habitus parallels this shift as evidenced by the flattened and broadened tail and limbs.

Based on these characters, we recognize three evolutionary lines within the genus. Species of Group I are characterized by numerous *Gekko*-like, undivided scansors on all digits. Members of Group II also have well developed scansors on almost all the undersurface of the digit, but a few subterminal scansors are divided. The tail in species of Group I and Group II is subcylindrical, without lateral flanges or spines. Species of Group III are characterized by a reduced number of scansors, with the terminal as well as a few subterminal scansors divided, and by being more depressed with flatter and broader tail. Three of the four new species of *Lepidodactylus* described here are members of the *pumilus-oorti* group (Group I) and one of the *guppyi-pulcher* group (Group II). Additional changes which are evident but more variable within these evolutionary lines involve breadth relative to length of dilated part of digit, the proportion of the toe covered by scansors, and the extent of webbing.

We accept Russell's (1972:56) hypothesis that evolutionary trends within the genus involve shifts from the basic combination of characters exhibited by some *Gekko*-like ancestor. Group I, which is thus the most primitive of the three groups, includes seven species (Table 1). If we assume that the *Gekko*-like ancestor was as large as nearly all living members of the genus *Gekko*, *L. magnus* would be the most primitive member in size, with *L. oorti* next. *L. magnus* also has long, slender digits and small webs between the digits. Based on these features, *L. pumilus* is the most advanced member of the group. The species is small and has extensive interdigital webbing, shorter limbs and digits, and more broadly dilated digits. The difference in adult size between *L. magnus* and *L. pumilus* is also evidenced by hatchlings. Four hatchlings of *L. pumilus* (MCZ 141048–49 and 1135529–30) were 18.5–21.1 mm in snout-vent length, and four hatchlings of *L. magnus* (MCZ 98796–99) were 24.5–25.9 mm in snout-vent length.

The species of Group I occur in the islands of western Indonesia, New Guinea, and islands in the Torres Straits, the Solomons and Fijis in the Pacific, and Christmas Island in the Indian Ocean. *L. pumilus* of this group also is recorded from Hammond Island, offshore from Cape York, Australia, and may also occur in that region of Australia. It is also of some interest that the two species within this group which are most alike are *L. manni* (Fiji Islands in the Pacific) and *L. listeri* (Christmas Island in the Indian Ocean). Based on the small samples available, the two are so similar in the characters studied that they cannot be distinguished except as widely separated populations (see Key). The two populations may indeed be conspecific, but we have chosen not to synonymize them pending the availability of larger samples and field studies. It is also possible that recent human introduction accounts for one or the other of these populations.

Group II includes *L. guppyi, novaeguineae, pulcher, shebae,* and *gardeneri*—species with undivided terminal scansors on all digits, but with a varying number of subterminal ones divided. Within this group, *L. gardeneri* and *L. guppyi* comprise a closely related pair. The two differ most obviously in the extent of the development of interdigital webs (Table 1). *L. pulcher* and *L. novaeguineae* are another pair of related species which differ from each other in the number of scansors, the size of the eye relative to the snout length, and the length of the hind limbs relative to the axilla-groin distance (Table 1).

The species of Group II have a more restricted distribution. They are known from northern New Guinea, the Solomons, Admiralties, Bismarks, and Rotuma Island north of the Fijis.

Group III includes those species which are most advanced with respect to digital structure in terms of Russell's hypothesis. Several distal scansors, including the terminal one, are divided, and scansors tend to be lost from the basal part of the digits and to be reduced in number. The tail is more depressed and is broader.

The species of Group III include four endemic to the Philippine Archipelago and the widely distributed *L. lugubris-woodfordi* complex. Populations in this complex range from islands of the Indian Ocean and India to the western shores of the New World. The populations in Central America and South America, however, are apparently the result of very recent transport by man. In the past, some samples from various populations throughout the range have been referred to *L. lugubris* by numerous authors, some have been described as distinct species only to be placed in synonymy by later authors, and still others from New Guinea, Philippines and other Pacific islands have been referred to *L. woodfordi*. Boulenger's (1887:334) brief description of *L. woodfordi*, based on a single specimen, was erroneously related to *L. guppyi* rather than *L. lugubris*. *L. woodfordi* and *L. lugubris* belong to the same evolutionary line and, in terms of characters used here, may possibly differ in color pattern and degree of flattening of the tail, but little else (Table 1). Adequate samples from numerous populations throughout the Pacific region must be carefully studied and compared to determine the variability between and within the populations before the usefulness of these characters and the validity of these two named species, or the possible existence of additional races or species, can be finally determined.

The distributional pattern of the four species which inhabit Papua New Guinea is also of interest because of the similarity in basic features with those seen in some of the Papuan species of the genus *Sphenomorphus* (Scincidae) such as *solomonis, nigrolineatus, cinereus,* and *brunneus* (Greer 1973; Greer and Parker 1974). *L. novaeguineae* and *S. solomonis* are recorded only from low to moderate elevations along the north coast; *L. magnus, S. brunneus,* and *S. cinereus* are known from the central mountains; and *L. orientalis* and *S. nigrolineatus* are known from the Central District on the south coast, east of the Gulf of Papua. The fourth species of *Lepidodactylus*, *L. pumilus*, is found in the Western District, west of the Gulf of Papua, and on the islands in the Torres Strait.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XLI, No. 9, pp. 267–280; 3 figs., 5 tables. October 20, 1977

UNIVERSITY OF MICHIGAN
1977
SERIAL-CURRENT SERVICE

ELEPHANT SEALS BREEDING ON THE MAINLAND IN CALIFORNIA

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Abstract: A northern elephant seal gave birth on the mainland at Año Nuevo Point, California, in 1975, the first mainland birth for this species in this century. Seven females gave birth in 1976 and 16 in 1977. The initiation of breeding in this location was apparently precipitated by crowding on the Año Nuevo Island rookery, less than 1 km away. The new breeding area shows signs of increasing rapidly in size. Two hundred and forty-five thousand tourists attempted to view the seals during the last three years; 106,000 were taken on tours. The animals did not appear to be disturbed by the presence of humans in plain view at a distance of 10 m or more.

Introduction

Northern elephant seals, *Mirounga angustirostris*, breed on offshore islands along the coast of California and Baja California, Mexico. Except when sick or injured, they have rarely been observed on the mainland during this century. However, the population has increased so dramatically during the last decade that space on islands in northern California has come to be in short supply. Male elephant seals began to appear on the mainland directly across a narrow channel from the rookery on Año Nuevo Island, California, during the 1967 breeding season (Poulter and Jennings 1966). They have been seen here in every subsequent breeding season and their number has steadily increased. In 1975, a female came ashore and gave birth on the mainland. To our knowledge, this was the first northern elephant seal born on the continental mainland during this century. The cyclic, predictable appearance of these huge marine mammals on Año Nuevo Point, a state reserve that is open to the public, has attracted thousands of tourists from nearby metropolitan areas. They have jammed the reserve in recent winters in an attempt to view and photograph the seals. Various confrontations between seals and people, ranging from humorous to dangerous, have occurred.

The purpose of this paper is to trace the history of elephant seals on the mainland in this area, to present data which enables us to speculate on how and why breeding began here, and to discuss the implications of this extension in breeding range for these animals and man.

To fully appreciate the recent appearance of

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elephant seals on the mainland, one must consider this development in the context of the species' history over the last 175 years. Thousands of elephant seals existed at the beginning of the 19th century before sealing began. Their breeding range extended from Cabo San Lázaro in Baja California, Mexico, north to Point Reyes, California (Scammon 1874). However, in the space of about 40 years, the elephant seal population was decimated by sealers who killed them for their oil. By 1860, the population was so severely reduced that sealing was no longer economically feasible and, in 1869, the species was considered virtually extinct. The nadir of the elephant seal population was around 1894 to 1900 when less than 20 individuals survived on a single beach on remote Isla de Guadalupe, an oceanic island approximately 300 km off the coast of Mexico (Bartholomew and Hubbs 1960).

In 1922, the species was given protection by the government of Mexico. The United States government gave similar protection a few years later. The number of elephant seals has been increasing logarithmically ever since. They now reoccupy most of their former range. Immigrants from the parent colony on Isla de Guadalupe began to recolonize islands along the coast of Mexico and southern California during the period 1930 to 1950. Colonies in northern California were established on Año Nuevo Island in 1961 (Radford, Orr and Hubbs 1965) and on Southeast Farallon Island in 1972 (Le Boeuf, Ainley and Lewis 1974).

The Año Nuevo Island rookery seems to have reached its carrying capacity. The number of pups born on Año Nuevo Island has increased every year since the first two pups were born in 1961 (Le Boeuf 1977). In 1977, 750 pups were born; at least this many females were present as well as 266 breeding-age males. During the peak of the breeding seasons in 1975, 1976 and 1977, the two sandy beaches on the island were crowded with females, their pups and adult males. Few additional males could have been accommodated on these preferred breeding areas (Le Boeuf and Briggs 1977). Evidently, some animals were affected by the crowded conditions and bred elsewhere. Many of the animals that colonized Southeast Farallon Island, 89 km to the north, during the period 1972 to 1977, were immigrants from Año Nuevo Island (Le Boeuf, Ainley and Lewis 1974; Harriet Huber, personal communication). Breeding began on the Año Nuevo mainland during this same period.

METHODS

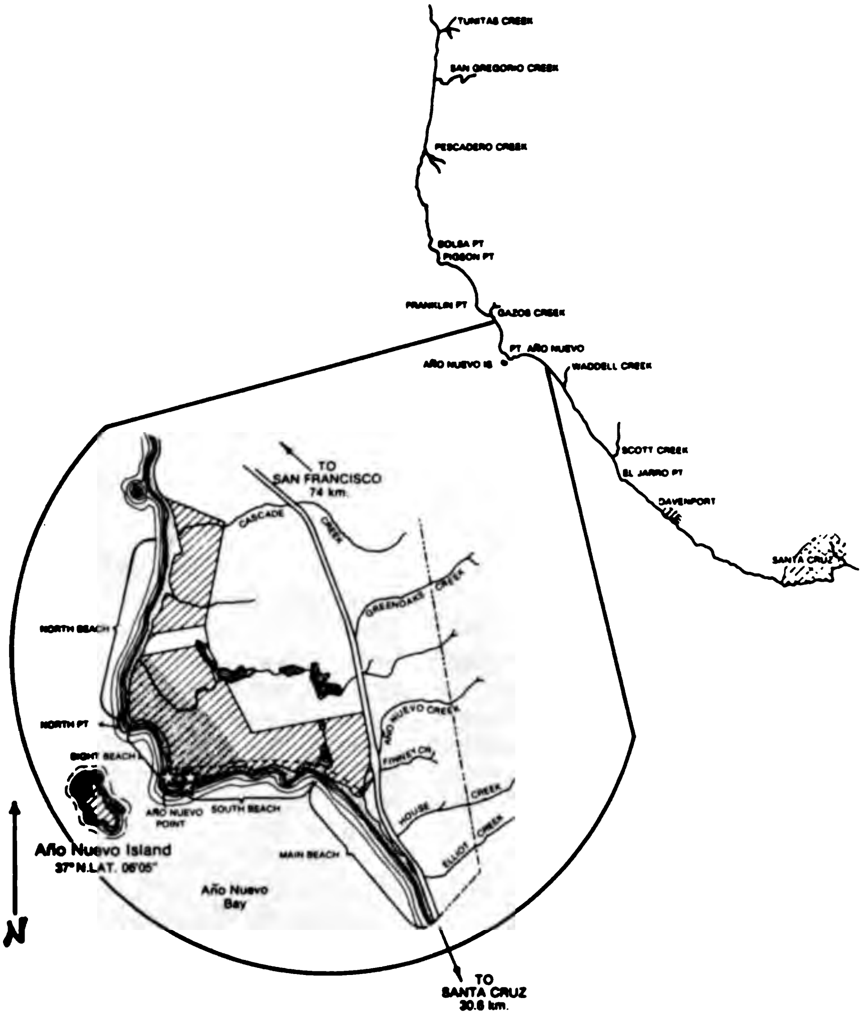
Año Nuevo Island is located 30.6 km north of Santa Cruz, California. It is separated from the mainland point that juts out to sea by a 0.8-km channel. The study area is shown in Figure 1.

Periodic censusing of the Año Nuevo Mainland began during the 1968 breeding season (1 December through 15 March) as an adjunct to systematic studies of the northern elephant seal on Año Nuevo Island by Le Boeuf and collaborators from the University of California at Santa Cruz (e.g., Le Boeuf and Peterson 1969; Le Boeuf and Briggs 1977). This paper covers censuses taken on the mainland during the period 1968 to 1977.

The number of censuses varied greatly from year to year. The mean number of censuses per breeding season from 1968 to 1974 was 22 and the range was from seven in 1973 to 50 in 1971. Counts were made at various times of day, from late December until the first week in March, by walking the beach or from the island using a 15–60 power spotting scope. In 1975 and 1976, censuses were taken one to three times a week, usually in the mornings between 0900 and 1100 hours, by walking the length of the beach and searching the dune area. On several occasions, a second census was taken in the late afternoon. In 1977, censuses were taken daily at 0900 throughout the breeding season.

In our censuses, we distinguished males from females and adults from pups and juveniles. Breeding-age males were separated into four categories: adults (8+ years old), subadult or SA^4 (7–8 years old), SA^3 (6–7 years old), SA^2 (5 years old) and SA^1 (4 years old). SA^1 males are rarely observed on land during the breeding season (Le Boeuf 1974).

In addition to counting and categorizing the animals, we were able to keep a record of individuals present. Studies on the island necessitated marking all males. This was done by bleaching a name or number into the pelage on both sides of each animal's back as soon as it arrived (Le Boeuf and Peterson 1969) and by attaching numbered plastic tags into the interdigital webbing of the hindflippers (Le Boeuf, Ainley and Lewis 1974). Since most males moved back and forth between the island and the main-



IGURE 1. A schematic drawing of the Año Nuevo mainland and Año Nuevo Island. Stars indicate the location that females
e birth in 1976. Most of the females that gave birth in 1977 congregated in a harem on the east side of Año Nuevo Point. The
e reserve property is lined and the sand dunes are stippled.

d, most seals observed on the mainland were
eady marked and could be identified individu-
. When necessary, marking and tagging were
done on the mainland. In 1975, 1976 and
7, females and their pups were given indi-
ual marks (names) and tags denoting their re-
onship and the time and place of birth. Thus,
ddition to determining the number and com-
ition of animals present each day, we could
identify individuals and follow them from
to day and from year to year.

ince 1975, we have paid special attention to
roductive behavior and pup mortality. We
orded the following data on females: the time of arrival, the date and location of parturition, the sex and condition of pups, the frequency and date of each copulation as well as the male involved, and the date of departure. If an arriving female was tagged, its age could be determined. The location of parturition of all females was determined as well as their nursing behavior. We noted the reactions of females to their own pups and to those of other females. The incidence and manner of pup deaths were recorded.

RESULTS

Number. The number of elephant seals observed on the mainland during the breeding sea-

TABLE 1. NUMBER OF ELEPHANT SEALS ON AÑO NUEVO MAINLAND (ML) AND AÑO NUEVO ISLAND (ANI) DURING A TEN-YEAR PERIOD.

Breeding season	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Highest daily census of males on ML	7	6	3	10	6	18	26	45	64	151
Number of different males on ML per season	7	11	7	15	16	38	44	94	148	320
Number of different males on ANI per season	103	120	125	136	146	180	146	143	227	266
Number of females on ML at peak season	0	0	0	0	0	0	0	1	7	16
Number of females on ANI at peak season	178	219	291	296	341	360	426	556	687	740

son increased dramatically from 1968 to 1977 and coincided with a rapid increase in the size of the colony on the island. Table 1 shows that both the highest daily census and the number of different males observed in a season increased significantly during the study period. No females were observed prior to 1975. The rapid growth of the Año Nuevo Island population is reflected by the annual increase in number of females counted at peak season. The number of pups produced each year was approximately the same as the number of females counted at peak season (Le Boeuf and Briggs 1977).

Distribution. Figure 1 shows the location on the mainland where the majority of seals were observed and the relationship of this area to the island. During the 1967 season, males were observed on Bight Beach and near Año Nuevo Point (Poulter and Jennings 1966). In later seasons the seals occupied an increasingly larger area of the mainland with some individuals appearing beyond the limits of the map shown in Figure 1. However, the majority of animals were observed between North Point and the eastern edge of South Beach; the heaviest concentration was usually in the immediate vicinity of Año Nuevo Point. In recent years movements into the sand dune area became more frequent. On several occasions, males were observed as much as 0.5 km back into the dunes. In 1977, the dunes near Bight Beach were a gathering place for numerous subadult males.

In 1972, males began hauling out on beaches beyond the boundaries of the state reserve. One early excursion was recorded on national television; a mature bull surfaced on the Pebble Beach Country Club golf course, 72 km from Año Nuevo Island, during the middle of a tournament. He was back on the island the following day. In the same year, one subadult male made numerous trips to Southeast Farallon Island. He and two other males from the Año Nuevo colony became permanent residents of this rookery the following year (Le Boeuf, Ainley and Lewis 1974). In 1974, another bull took up residence for approximately three weeks on the main beach near the park entrance which borders the southern edge of the reserve. In 1975, 1976 and 1977, males were sighted on several other beaches in the vicinity, extending from Bean Hollow Beach, 14.5 km to the north, to Davenport Landing, 14.5 km to the south. Other public beaches where males were observed for several days include: Gazos Creek, Waddell Creek, Scott Creek, and Greyhound Rock (Figure 1). Most of the males observed on these peripheral beaches were mature, i.e., classified as an adult or near adult (SA^4).

Prior to the arrival of females, spacing between males on the beaches was 3–4 meters or more. Males were rather evenly distributed on Bight Beach, near Año Nuevo Point, and on South Beach. When females began to give birth in the vicinity of Año Nuevo Point (Figure 1), males began to concentrate in this area. This was especially noticeable in 1977 when a harem composed of 12 females formed in this area.

Composition. Who were these males that fre-

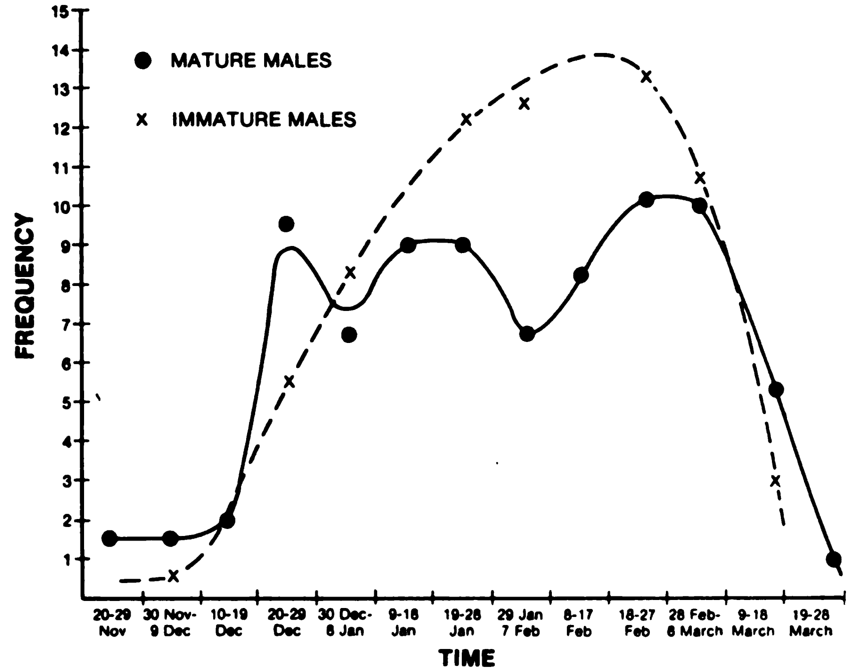


FIGURE 2. The mean number of mature and immature males on the Año Nuevo mainland calculated at 10-day intervals during the 1975 breeding season. A mature male is one who is approximately 8 years old or older.

quented the mainland? Because nearly all of them were marked individually and daily records of their whereabouts were kept, it was evident that males observed on the mainland were associated with the island population. Indeed, many males moved back and forth across the channel on a daily basis. For example, in 1976, 65 percent of the males marked on the island were observed at least once on the mainland; all males observed on the mainland were also seen on the island.

Table 2 shows that both mature and immature males were present on the mainland, with the former predominating in early years. This discrepancy may have been due in part to the fact that it was more difficult to mark all immature males because they continued to arrive throughout the season. In addition, a greater effort was made to mark adults in early years. On the island, the ratio of mature males to immatures was very close early in the study period. By 1975, immatures were more prevalent than matures on both the island and the mainland. The ratio of adults to immatures on the island in 1974 is inconsistent with other years because of a reduced effort to mark young males. In general, the age composition of males observed on the mainland reflected the age range of males that were present on the island.

Mature males tended to outnumber immature

TABLE 2. NUMBER OF MARKED MATURE (ADULTS AND SA^4 MALES, 7 YEARS OF AGE OR OLDER) AND IMMATURE BULLS (SA^2 AND SA^3 MALES, LESS THAN 7 YEARS OLD) HAULED OUT ON AÑO NUEVO MAINLAND AND ISLAND IN TEN CONSECUTIVE BREEDING SEASONS.

Area	Age Category	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Mainland	Mature	4	9	5	8	10	23	31	46	55	58
	Immature	2	2	2	7	6	15	11	48	93	262
Island	Mature	41	46	50	51	50	74	89	69	75	71
	Immature	48	56	64	60	77	92	49	74	152	195

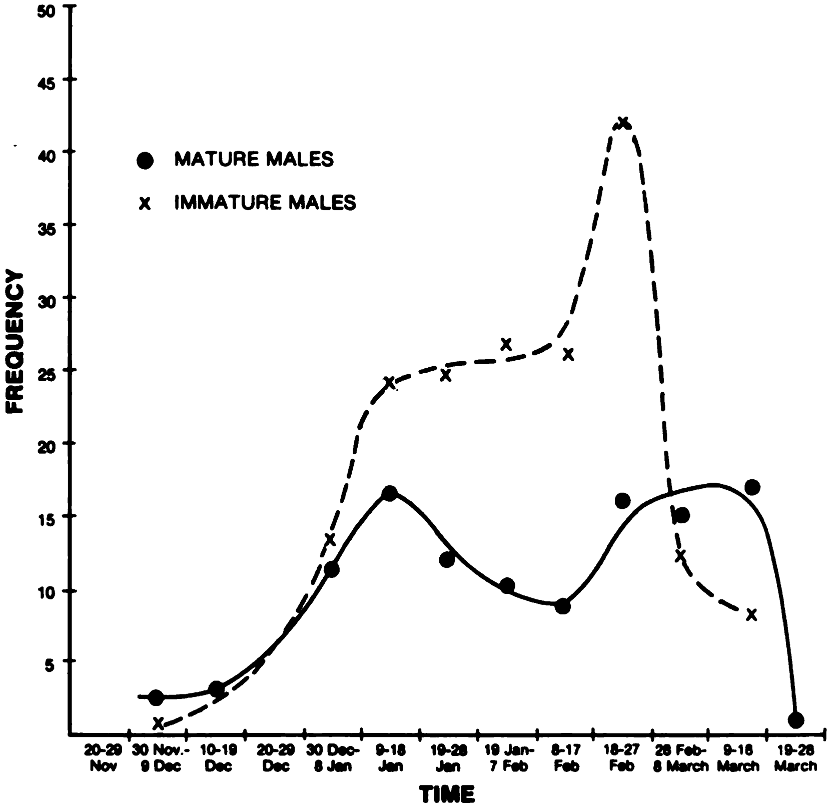


FIGURE 3. The mean number of mature and immature males on the Año Nuevo mainland during 10-day intervals in the breeding season.

males during the beginning and end of each breeding season. The distribution of males on the mainland in 1975 and 1976 is shown in Figures 2 and 3. This difference in distribution with age was due to multiple causes. One strategy of adult males was to rest on the mainland in December and early January and then move to the island in late January when females began coming into estrus. Some individuals were very predictable and repeated this pattern from one year to the next. Movement from the mainland to the island by the older, more dominant males was particularly evident in late January and early February. This pattern was less in evidence in 1977.

The peak number of immature males on the mainland occurred in mid-February and coincided with the time of highest copulatory activity on the island (Figures 2 and 3). This pattern resulted in part from the fact that many young males were chased off the breeding beaches on the island by older, more aggressive bulls when the majority of females came into estrus. T the young males were forced to haul out on v ous non-breeding areas on the island and on mainland. This pattern of immature males re ing a peak on the mainland in mid-February most obvious from 1974 to 1976. Figures 2 a also show that immature males arrived on mainland later in the season, and they left ea than adult males.

Once females began to appear on the m land, the most dominant males tended to ren near the females until the latter had given bi nursed their pups, copulated and returne sea. Only then did the males cross the chann compete for females on the island. At seas end, when all females had departed from th land, some males returned to the mainlan rest before going out to sea.

Another strategy that was observed, part larly in early years, was for adult males to on the mainland for several days or even a weeks after losing an important fight on th

TABLE 3. REPRODUCTIVE SUCCESS OF MAINLAND-OBSERVED MALES ON AÑO NUEVO ISLAND.

Breeding season	1968	1969	1970	1971	1972	1973	1974	1975	1976
Number of different males on ML per season	7	11	7	15	16	38	44	94	148
Number of different ML-observed males that copulated on ANI	2	4	4	4	6	12	14	39	34
Percent copulations by ML-observed males on ANI	5	4	20	no data	19	31	6	68	42

land. Several former harem masters on the island, deposed after commanding a harem containing hundreds of females for as long as six weeks, recuperated in exile on the mainland. The sight of bloody bulls prompted local residents and tourists to refer to the mainland as "loser's beach." This is misleading. Clearly, some males were resting after having been defeated in a fight, but many of them on the mainland were by no means losers from the point of view of aggression or reproductive success. Table 3 shows that at least a quarter of the males observed on the mainland each year copulated on the island. In 1975 and 1976, males that had been seen on the mainland accounted for 42 and 68 percent of the copulations observed on the island. Furthermore, in every year of the study, at least one male observed on the mainland was among the 10 highest ranking bulls on the island. The correlation between rank and reproductive success among males is high and positive (Le Boeuf 1974). Finally, we can reiterate that the majority of the males in the Año Nuevo population were observed both on the island and on the mainland.

As the total number of males on the mainland increased over the course of the study period, males began to arrive earlier and stay later in the season each year. In 1968, the first male arrived on 11 January and the last one left on the first of March. In 1977, the first male arrived on 15 November and the last one departed on 26 March.

Non-reproductive behavior of males. There were no obvious differences in the behavior of mature and immature males on the mainland. Most of them spent their time sleeping on the dry sand near the upper edge of the beach. A few rested among the sand dunes. Threatening behavior, chasing and an occasional fight were frequent activities of waking animals even before females began to appear. After the females arrived, aggressive encounters were most frequent in their vicinity. Young males were not as aggressive as older males and one might say that they "played" like adults in these aggressive confrontations. On several occasions, males attempting to land were rebuffed by the threats of dominant males on land—the result was that they landed further up or down the beach. This pattern of competition for social rank is typical of males on the island (Le Boeuf 1971, 1974). Many movements on the mainland consisted of simply going in and out of the water. Most often, this was in response to aggressive encounters with other males, but the animals also entered the water to cool off in hot weather. Males were often observed swimming along the surf line checking out the opposition, chasing off subordinates with the characteristic vocal threat, and remaining silent and low in the water when swimming past a dominant male.

Duration of stay. The duration of each male's stay on the mainland was variable. Some males were sighted on the mainland only briefly. Others crossed the channel several times a day and were sighted at several disparate locations. Some individuals remained in virtually the same location for several weeks. For example, in 1974, an aging bull named Star caused us considerable trouble because he spent most of the breeding season sleeping on a narrow sandy access road to the beach, the route that we had to drive over in order to launch our boat to the island. The presence of females on the mainland after 1975 did not appear to change significantly the duration of the mainland haul-out for the majority of males; the exceptions were the few males who did most of the breeding.

Reproductive activities on the mainland. On 21 January 1975, a pregnant female hauled out near Año Nuevo Point (Figure 1). Three days later she gave birth to a female pup. A pregnant female had attempted to land here in 1973 but she was frightened off by tourists. The birthplace and age of the new mother were unknown. She and her pup were tagged and named, Bertha and Blue, respectively. Bertha nursed her pup daily for 30 days. A mature male, Baja, remained near here throughout the nursing period and kept all other suitors away. He alone, apparently, copulated with her on the same day that she returned to sea. All of these activities were similar to those seen on the island (Le Boeuf, Whiting and Gantt 1972), except that they were performed under the watchful eyes of thousands of tourists (e.g., San Francisco Chronicle, 29 January 1975; San Jose Mercury, 18 March 1975).

The 1976 breeding season. Bertha and six other females gave birth on the mainland in January, 1976. Three additional females were observed and marked in the area early in the month but they remained for only a day or two before departing.

The age and birthplace of only one mainland female was known. She was a three-year-old, born on Año Nuevo Island and tagged (Green tag 1961) as a one-month-old weaned pup on 13 February 1973. Her pup died when it was 11 days old after being trampled by a charging bull. This female left the area later in the day.

Besides the above, another female gave birth to a full-term stillborn. Thus, two pups died out of the seven born on the mainland. The other five pups survived to weaning and remained on the mainland for a few weeks after all adults had departed.

An additional pup, a 1½-week-old orphan found at Drake's Bay near Point Reyes, was transported to the Año Nuevo mainland on 26 January by representatives of the California Marine Mammal Center, Fort Cronkhite, California. They placed the orphan alongside Bertha who was pregnant. She adopted the alien pup, allowing it to suckle along with her own pup who was born later in the evening. Both the adopted orphan and the filial pup survived to weaning age. The topic of adoption will be treated in more detail in a later section.

In 1976, mainland females gave birth in three separate locations (Figure 1): three gave birth on the beach just north of Año Nuevo Point, two on South Beach and two in the sand dunes, approximately 20 m inland from South Beach. Once females landed and gave birth they tended to remain in the same place throughout the 3–4 week nursing period without ever entering the water. This is characteristic of all nursing elephant seals (Le Boeuf, Whiting and Gantt 1972). The female whose pup was born dead was an exception. She was observed going in and out of the water several times as well as moving from one mainland harem to another.

The most dominant male on the mainland was named Up and he spent most of the season near the females on Año Nuevo Point. He alone copulated with both females that came into estrus. The next two males in order of dominance were SRI–236 and Atom. They positioned themselves near the females on the South Beach and near those in the dunes, alternating positions from time to time, particularly early in the season. Atom copulated with one female and SRI–236 copulated with two other females in the area. The three top-ranking males on the mainland were all adults. SRI–236 was ten years old, having been born and tagged on Año Nuevo Island in 1966 (Poulter and Jennings 1966). He was next seen on the island during a breeding season in 1971. Up and Atom were approximately the same age, and they were first observed on Año Nuevo Island in 1972. All three males returned to the island in subsequent breeding seasons and all of them were first observed on the mainland in 1974. The social behavior of other males on the mainland was concentrated around the breeding females and tended to be similar to that displayed by males competing on the island.

The 1977 breeding season. The number and distribution of males and females on the mainland underwent an obvious change in 1977. The population more than doubled, and for the first time a harem formed on the mainland at Año Nuevo Point consisting of 12 females at peak season. The number of males observed in the area was more than double that of the previous year, the increase being primarily in the subadult male category. The older, larger males concentrated on Año Nuevo Point near the female harem. Subadult males were more widely scattered except for a group of 50 to 60 individuals that congregated regularly in the sand dune area near the center of Bight Beach.

Sixteen females gave birth on the mainland in 1977, the original female, Bertha, being one of them. All births occurred during the interval 12 January to 6 February. As in the previous year,

TABLE 4. INTERVALS IN DAYS BETWEEN FEMALE REPRODUCTIVE EVENTS ON THE ISLAND AND THE MAINLAND.

	Año Nuevo Island			Año Nuevo Mainland	
	1970[1]	1971[1]	1976[2]	1976[3]	1977[4]
Arrival to parturition	—	6.5 ± 1.4 (10)	6.3 ± 1.6 (29)	3.3 ± 0.8 (6)	4.0 ± 1.6 (14)
Parturition to 1st copulation	24.6 ± 3.4 (9)	23.4 ± 4.2 (12)	26.1 ± 1.8 (25)	23.8 ± 3.3 (4)	22.8 ± 2.2 (13)
Parturition to departure (nursing period)	27.9 ± 4.0 (12)	29.0 ± 5.0 (29)	27.3 ± 1.6 (48)	26.0 ± 2.7 (5)	25.9 ± 1.1 (14)
1st copulation to departure	3.3 ± 2.8 (9)	5.2 ± 2.2 (11)	3.1 ± 1.9 (27)	4.0 ± 3.5 (4)	3.6 ± 2.3 (13)
Arrival to departure	34.3 ± 3.6 (10)	34.6 ± 3.8 (9)	32.4 ± 2.8 (17)	27.8 ± 3.8 (4)	29.9 ± 1.7 (14)

[1] From Le Boeuf, Whiting and Gantt (1972).

[2] Unpublished data collected by B. Le Boeuf, K. Panken, M. Pierson and J. Reiter.

[3] Excludes Green tag 3503 who gave birth and lost her pup. She did not nurse until 19 days later when she adopted a weaner. She departed 38 days after parturition and was on the mainland a total of 41 days.

[4] Excludes two females who abandoned their pups, one on the day it was born and the other seven days later. They both went to sea on the day they abandoned their pups.

several additional females landed early in January but did not remain in the area long nor did they give birth.

Besides Bertha, only one female from the previous year returned to the mainland to give birth (Green tag 3503). Two females that gave birth on the mainland in 1976 gave birth on the island in 1977 (Green tags 1861 and 3501). One female that gave birth on the mainland in 1977 (Green tag 1880) had given birth on the island in 1976. Of the three females that switched locations, two were three-year-olds who had lost their pups in the earlier year.

Tags on four females revealed that they had been born on Año Nuevo Island in 1973 and 1974. Thus, three females were primiparous three-year-olds, and one of them was a four-year-old.

Four females did not join the harem on Año Nuevo Point (Figure 1). Bertha and an unmarked female gave birth in the dunes approximately 100 meters east of the harem at Año Nuevo Point. However, Bertha entered the harem site before leaving the rookery. A three-year-old female and another female (Green tag 4543) gave birth on South Beach approximately 50 meters east of the harem.

There were no pup deaths on the mainland in 1977.

A male named BTLF (Green tag 3405) dominated all other males on the mainland, and he was involved in 60 percent of the matings observed. He was the first male to mate with 12 of the 16 females present. Most of the copulations by other males were performed while BTLF was engaged in combat with a challenger. BTLF was retagged on Año Nuevo Island during the 1975 breeding season; his earlier tag broke and could not be read. He copulated 29 times on the island in 1976 and was responsible for 4.7 percent of the matings observed. Up, the alpha male on the mainland in 1976, returned to the mainland in 1977 but copulated only once.

Female vital statistics. A comparison of intervals between various reproductive events on the mainland and the island reveals several differences (Table 4). For nearly every comparison the interval is shorter for mainland females than for females giving birth on the island. Compared to island females, mainland females gave birth sooner after arriving, they copulated sooner after parturition, they nursed their pups at least one day less, and they spent less total time on land during the breeding season. All comparisons between the 1976 island data and the 1977 mainland data are statistically significant (*t-tests*, $p < .05$) except for the interval, first copulation to departure.

Sex ratio of pups. Of the 24 pups born on the mainland during 1975 to 1977, 10 were males and 14 were females. The sample size is too small to permit a meaningful test for a significant deviation from the 50:50 sex ratio. The sex ratio of pups born on the island has not deviated signifi-

TABLE 5. THE FREQUENCY OF VARIOUS TYPES OF NURSING RELATIONSHIPS OF FEMALES ON THE MAINLAND.

	1976 (N = 7)	1977 (N = 16)	Both years combined (N = 23)
Nursed own pup to weaning age			
a. exclusively	2	6	8
b. and an alien occasionally	0	3	3
c. and an alien as well	2	5	7
Nursed an alien after losing own pup			
a. exclusively (adoption)	1	0	1
b. occasionally			
Did not nurse (because pup died, was abandoned, lost or stolen)	2	2	4

cantly from unity in recent years (Le Boeuf and Briggs 1977). It is notable that all four three-year-old females gave birth to female pups; a four-year-old female gave birth to a male.

Maternal behavior. The most frequently observed nursing relationship in elephant seals is one in which the mother nurses her own pup to weaning and rejects the suckling attempts of alien pups. However, several deviations from this pattern occur (Le Boeuf, Whiting and Gantt 1972). Indeed, complications in the nutritive relationship between females and pups on an elephant seal rookery were quite evident in the small and, hence, easily observed aggregation of females breeding on the mainland. Although it is beyond the scope of this paper to analyze this complex phenomenon in detail, we will describe some of these relationships to give the reader an appreciation for the range of possibilities observed.

In 1976, an aggressive female with pup stole the newborn of a neighbor and nursed it, plus her own pup, to weaning age. The neighbor remained in the harem without nursing for 19 days and then adopted a weaned pup on the day its mother left the harem. She nursed the large weaned pup, a male, for 20 days. In contrast, two other females departed the area on the day their pups died. Bertha, as we have already mentioned, adopted an orphan before she gave birth to her own pup; she nursed both pups to weaning age. Only two of seven females nursed their own pups exclusively.

Additional complications were observed in 1977. Although the majority of females nursed only their own pups, five females nursed an alien pup in addition to their own. One of them involved the serial adoption of two pups. While nursing her own pup, this female adopted an orphan and nursed it for three days where upon she adopted another orphan, which she nursed for 12 days. Bertha, again, fostered a pup in addition to her own. Two females that gave birth within one day of each other nursed each other's pup as well as their own. Finally, two females abandoned their pups one and seven days after parturition, respectively. Their pups were nursed to weaning age by two different females with pups of their own. In both years, it was obvious to us that pups sharing a mother weighed less at weaning age than pups that suckled a female by themselves. However, weights were not obtained which would confirm this impression.

The variety of nursing relationships observed on the mainland and the frequency of their occurrence are summarized in Table 5. It is interesting to compare these figures with those collected on Año Nuevo Island in 1970 and 1971 by Le Boeuf, Whiting and Gantt (1972). In this study, 72 percent of the females in a sample of 50 nursed their own pups to weaning age (alone or in addition to an alien pup). This figure is similar to the figure obtained on the mainland in 1976 and 1977, i.e., 78.3 percent of the 23 females nursed their own pups to weaning age. However, the percentage of adoptions was more than twice as high on the mainland as on the island, 34.8 percent of the females adopted a pup on the mainland compared to 14.0 percent on the island. We conclude that adoption occurs if a female nurses a pup consistently for one or more days regardless of whether she is already nursing her own pup. The duration of fostering observed on the mainland ranged from 7 to 26 days. Ten percent of the females in the island study did not nurse any pup after giving birth as compared to 17.4 percent in the mainland sample. None of these females were ever observed copulating. Finally, in the larger population on the island, a few females each year permitted several pups to attempt to nurse at the same time. This permissiveness was not observed in mainland females, perhaps because there were fewer orphans present at all times.

Non-breeding season observations. Prior to

1976, the only observations of elephant seals on the mainland during the non-breeding season was in March and April. An occasional weaned pup swam across the channel and rested on the mainland for a few days, or a molting juvenile appeared for an equally short stay. However, in June 1976, many young males, who normally molt on the island at this time of year, were observed resting on the mainland at Bight Beach (Figure 1). For example, on 11 June, 20 males were resting on the mainland and 25 were in the water offshore. The highest number counted onshore was 30 on 26 June (M. Bradeen, personal communication). Elephant seals are observed on Año Nuevo Island at all times of the year (Le Boeuf, Ainley and Lewis 1974). Perhaps the presence of subadult males in June 1976 signals the beginning of a similar pattern on the mainland.

The reaction of seals to humans. Prior to the 1974 breeding season, the presence of elephant seals on the mainland attracted little attention. Only a few local residents and nature lovers knew about the seals and paid much attention to them. The distance of the seals' resting place from the parking lot was also a deterrent. Año Nuevo Point is about a 30-minute walk from the park entrance, and it can be cold, wet and windy in winter. However, just before the start of the 1974 breeding season, a national magazine called attention to this unusual spectacle and recommended it to its readers (Sunset Magazine, December 1973). Suddenly, this rather desolate area was flooded with hundreds of tourists. The understaffed and underfinanced Department of Parks and Recreation was not prepared to deal with this huge influx of people. During that winter, people were free to roam the beaches and dunes, and only the number entering the reserve was controlled. On one fair-weather weekend, as many as a thousand people strolled the beaches and sand dunes in the vicinity of Año Nuevo Point. Each male elephant seal was surrounded by a circle of onlookers and amateur photographers. Families with small children walked too close to bulls weighing as much as 2–3 tons, unaware of the danger. Some people gigged, prodded and threw pebbles at these giants in order to get more interesting photographs. The public had not been informed that these animals might be dangerous or sensitive to human disturbance. In retrospect, it is surprising that no one was injured. We know of several cases where people have been bitten by elephant seals at other places (the second author is one of them).

It is equally surprising that the seals, all males that year, were so impervious to this constant attention and frequent harassment. Their typical response was to sleep and occasionally flip sand on their backs. When irritated, they gave a low-level open-mouth threat and increased the frequency of their sand flipping habit (Heath and Schusterman 1975). When pushed even further, some bulls reared up and bellowed the species-typical threat vocalization. Some charged the attacker for a distance of a few meters. Despite being provoked most males remained on the beach. Even those young males who backed down and were hounded into the water returned to the beach a short time later. Regardless of the throng of people in the area, the seals appeared to be primarily interested in each other's movements. Several times it looked as if a male was charging a human when in reality he was attacking another male behind the person. When the seals were not being disturbed or approached too closely, they seemed to ignore the humans in the area.

Disturbance to the seals in the park reserve was reduced considerably in subsequent years. Beginning in 1975, tourists were led on guided tours of the seals in groups of 20. Park rangers and student guides were informed about the animals, and were prepared to answer questions about them. A single path led through the sand dunes to overlooks near Año Nuevo Point and South Beach where the incipient harems were located. Tourists were restricted to the paths and overlooks and were prohibited on the beaches and dunes where the animals were abundant. Approximately 245,000 people came to view the seals during the winter months of 1975, 1976 and 1977; approximately 106,000 people were led on tours.

It is difficult to say whether a constant stream of tourists in plain view of the seals inhibited utilization of this area by the seals. Males did not appear to be affected very much even when harassed (a response that made them easy to slaughter in the last century). Females, on the other hand, are much more wary, especially when they first arrive and before they give birth. If disturbed during this period, females may reenter the water and either return to the same location later or give birth elsewhere. This pattern has been observed on the island in previous years (Le Boeuf, Whiting and Gantt 1972). We do not know whether females were frightened off by human activities on the mainland and, if so, the numbers that were affected. Since females often survey a potential breeding beach from the water before hauling out, this form of disturbance is difficult to monitor. Some females haul out and then leave. We know of at least three pregnant females that landed on the mainland in 1976 and subsequently departed before giving birth. A similar pattern was observed in 1977. We do not know what caused these females to leave, and we were not able to determine where they gave birth.

Once a female gives birth, her movements decrease significantly and she is not likely to abandon her pup even if disturbed or approached closely by a human. Under these circumstances, a female will flip sand on her back nervously, issue a vocal threat and then attack. She will bite, hold and shake the victim. Female bites can produce severe injury. We saw several instances on the mainland where tourists ventured close enough to females and their pups to provoke arousal of females and the threat reaction just described. When advised, park rangers increased the viewing distance between seals and humans and this form of disturbance and potential danger was eliminated. When humans and seals were separated by approximately 10 m or more, the seals appeared to acclimate to the presence of humans in plain view, and females did not show obvious signs of alarm. As far as we could tell, the response of females to their pups was not affected adversely by human presence, but this subject deserves systematic study.

DISCUSSION

The initiation of breeding on the Año Nuevo Mainland is a reflection of the continued growth and recovery of the northern elephant seal population following its near extinction in the last century. Indeed, the growth of the population has increased so rapidly of late that the Año Nuevo Island breeding beaches have become filled to capacity at peak season (Le Boeuf and Briggs 1977). It is this condition which seems to have precipitated breeding in what might be called a suboptimal area—suboptimal because the mainland was formerly a habitat in which the seals were subjected to predation from carnivores and coastal aborigines. Several lines of evidence lead to this conclusion: 1) females did not begin breeding on the mainland until the breeding beaches on the island began to be crowded (Le Boeuf and Briggs 1977); 2) during the same period, a new colony was formed on nearby Southeast Farallon Island, with most of the original settlers coming from Año Nuevo Island; and 3) on Año Nuevo Island, the first females to arrive at the start of the breeding season have been observed preventing later arriving females from landing (Christenson and Le Boeuf 1977) or forcing them to occupy peripheral positions in harems where pup mortality is higher (Le Boeuf and Briggs 1977).

Preliminary data suggest that it is the youngest females that begin breeding in new areas. Many of them are literally prevented from landing on breeding beaches or they are relegated to inferior locations by older, more aggressive females. Older females do this to enhance the probability of their own pups surviving (see Le Boeuf and Briggs 1977). A female is fully grown at six years of age; however, developing females usually give birth for the first time at age three, a few as early as age two. Subsequently, females give birth to a single pup annually (Le Boeuf, unpublished data). Most of the marked females breeding on Southeast Farallon Island from 1972 to 1977 were between three and six years old. For example, four of six known-age females.that gave birth in 1975 were four years old, the other two were three years old and five years old, respectively. As late as 1977, seven females out of 12 known-age newcomers were three or four years old (H. Huber, personal communication). On the Año Nuevo mainland, four of the known-age females that gave birth were three years old and one was four. Furthermore, observations of known-age females on Año Nuevo Island in 1976 by us, J. Reiter and M. Pierson revealed that over 50 percent of the females five years of age or less became separated from their pups, while less than 10 percent of the females six years of age or more lost their pups. Since mother-pup separation is the initial event in a syndrome culminating in pup mortality (Le Boeuf, Whiting and Gantt 1972; Le Boeuf and Briggs 1977), reproductive success, as measured by pup survival, is evidently lower in young females than in older females who are fully grown. Thus, it is obviously a reasonable strategy for young females to explore breeding in a peripheral place with more space, less competi-